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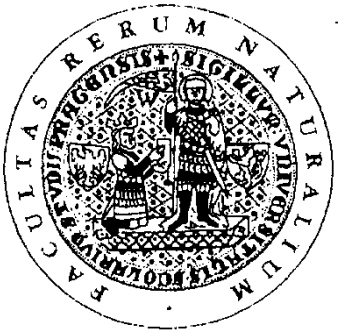

Vodní režim blatkových borů na Třeboňsku a vodní provoz jejich dominant

Water régime of *Pinus rotundata* dominated peatbogs in the Třeboň Basin and water relations of their dominant species

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Disertační práce

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AUTHOR´S CONTRIBUTION

A. Kučerová, nee Kolmanová, compiled the summary part of this thesis.
Articles I-IV: A. Kučerová was the main writer in all papers and she had the main responsibility for most of the field work.

I declare that this thesis or any part of it was never submitted to obtain any other academic degree.

PROHLÁŠENÍ

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Podpis

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ABSTRACT

The thesis was intended to fill the information gap in the ecohydrology of the *Pinus rotundata* dominated peatbogs in the Třeboň Basin Biosphere Reserve, Czech Republic by studying various aspects of their water régime (i.e., transpiration of the dominant tree species, soil water chemistry, retention ability). The study is based on regular monitoring of the water table, water discharge, soil water chemistry and precipitation (during 1995-2000, study sites Červené blato and Žofinka peatbogs). Additionally, the transpiration of adult *Pinus rotundata* trees was measured in the field during 1999-2000 at the experimental plot in the Červené blato peatbog (330 ha, 465–475 m a.s.l.).

Nowadays, the *Pinus rotundata*-dominated peatbogs represent almost natural (peaty) forests inside of otherwise human-made forest plantations. Long-term vegetation changes after natural disturbances such as windstorms, insect infestation and fire are only occasionally reported for the central European natural forests. Therefore the evaluation of vegetation changes after disturbances, typical of boreal forests, and their impact on peatbog hydrology has also been included in this thesis (study site Žofinka peatbog, 130 ha, 470–475 m a.s.l.).

Transpiration of the central European endemic tree species, *Pinus rotundata* Link, was measured by sap flow techniques (heat field deformation method) in individual trees, and scaled up to stand level. Adult trees tolerated well both short-term flooding during the growing season and drawdown of the water table to a depth of 60 cm below ground level. The maximum and mean daily transpiration rates were 3.0 and 1.8 mm per day. Scaled-up daily canopy transpiration was non-linearly related to potential evapotranspiration, thus demonstrating a limitation of transpiration under high evaporative demand, even when soil water supply was not limited. The seasonal total transpiration (25 April–20 October 2000, 180 days) amounted to 322 mm, or 62 % of the potential evapotranspiration over this period. This canopy transpiration was compensated by 319 mm of precipitation.

A *Pinus rotundata* dominated peatbog (Žofinka National Nature Reserve) was affected by "natural" disturbances: wind damage (1984), followed by a bark beetle attack, and fire (1994, 2000). The species composition of the windthrow–bark beetle affected sites and the undisturbed *P. rotundata* bog forest differed mainly in the shrub and tree layers. Canopy break-up resulted in the expansion of ericoid dwarf shrubs while the water table fluctuations were reduced. Most plant species characteristic of the *P. rotundata* bog forest occurred at the burned sites eight years after the fire, but in different abundances. The dominant tree of the former community (*P. rotundata*) was mostly absent. Compared with windthrow followed by bark beetle attack, fire promoted rapid expansion of the grass *Molinia caerulea*.

Soil water in both the undisturbed *P. rotundata* bog forest and the windthrow–bark beetle affected sites had a similar composition: very low pH (3.4 and 3.8, resp.), medium high P concentrations (0.16 and 0.18 mg/l, resp.), low concentrations of cations (2.70 and 3.98 mg/l of Ca^{2+}, 0.42 and 0.41 mg/l of $Mg^{2+}$and 0.92 and 0.51 mg/l of K^{+}, resp.) and inorganic nitrogen (NH_4-N 0.93 and 0.76 mg/l, resp.). During the growing period, the concentrations of soluble reactive phosphorus (SRP), total P, NH_4-N and pH increased as the groundwater table decreased. At the burned site, SRP, total P and NH_4-N soil water concentrations were by one order of magnitude higher than those in the *P. rotundata* bog forest, while the concentrations of K^{+}, Mg^{2+} and Ca^{2+} were about two times as high.

The water retention capacity of a raised bog, studied in the Červené blato peatbog, varied greatly during the year. The retention capacity depended on the actual position of the water table. It was relatively high in periods of a deep water table in summer (up to cca 70 mm per week). By contrast, when the water table was high (e.g., after heavy rains) the retention capacity was very low and almost all precipitation water was discharged from the peatbog. Similarly, the retention capacity of liquid precipitation was almost zero during winter.

ABSTRAKT

Tato práce je zaměřena na různé aspekty vodního režimu blatkových vrchovišť v Třeboňské pánvi (transpirace dominantního druhu, charakteristiky kolísání hladiny podzemní vody, chemismus půdní vody, vodní retenční schopnost). Část studie byla založena na dlouhodobém, pravidelném monitoringu hladiny podzemní vody (celkem ve 40 pozorovacích sondách), odtoku vody, srážek a chemismu půdní vody (v letech 1995-2003, studijní lokality NPR Červené blato a NPR Žofinka). Transpirace středoevropského endemického druhu – borovice blatky (*Pinus rotundata* Link) – byla měřena na experimentální ploše v NPR Červené blato (330 ha, 465–475 m n.m.) v r. 1999–2000.

V současnosti představují blatkové bory jedny z mála přírodě blízkých lesních porostů v Třeboňské pánvi. Dlouhodobé vegetační změny po přirozených narušeních jako jsou větrné polomy, přemnožení podkorního hmyzu a požáry jsou z přirozených lesních porostů střední Evropy uváděny jen zřídka. Vyhodnocení vegetačních změn po narušeních, jinak typických pro boreální lesy, a jejich dopad na hydrologii rašeliniště je další částí této práce (studijní lokalita NPR Žofinka, 130 ha, 470–475 m n.m.).

Transpirace borovice blatky byla měřena pomocí sledování toku vody v xylému (metoda deformace teplotního pole) na jednotlivých stromech (šest vzorníků) a přeškálována na porostní úroveň. Vzrostlé blatky snášely bez poškození krátkodobé zaplavení kořenového systému během vegetační sezóny i pokles hladiny podzemní vody 60 cm pod povrch půdy. Maximální transpirace porostu byla 3,0 mm za den, průměrná transpirace porostu za celou vegetační sezónu pak 1,8 mm za den. Denní transpirace porostu byla nelineárně závislá na potenciální evapotranspiraci, tzn. rychlost transpirace byla limitována při vysoké výparnosti ovzduší i přes dostatečnou zásobu půdní vody. Celková transpirace porostu za vegetační sezónu (25.4–20.10. 2000, 180 dní) byla 322 mm, resp. 62% potenciální evapotranspirace za toto období. Tato transpirace byla kompenzována 319 mm srážek.

Původní zachovalé blatkové bory v NPR Žofinka byly ovlivněny přirozenými disturbancemi: polomem (1984), následným přemnožením podkorního hmyzu a požáry (1994 a 2000). Na plochách narušených polomem a žírem podkorního hmyzu a v nenarušeném fragmentu blatkového boru se druhové složení lišilo hlavně u keřového a stromového patra. Rozpad stromového patra vedl k rozvoji erikoidních keříčků a ke snížení kolísání hladiny podzemní vody. Většina druhů původního blatkového porostu se vyskytovala na plochách zasažených požárem po 8 letech, ale s jinou četností. Ve srovnání s polomem následovaným žírem podkorního hmyzu požár vyvolal rychlé šíření bezkolence (*Molinia caerulea*).

Půdní voda v nenarušeném blatkovém boru a na plochách ovlivněných polomem a žírem podkorního hmyzu měla podobné složení: velmi nízké pH (3,4 a 3,8, resp.), středně vysoké koncentrace P (0,16 a 0,18 mg/l, resp.), nízké koncentrace kationtů (2,70 a 3,98 mg/l Ca^{2+}, 0,42 a 0,41 mg/l Mg^{2+}a 0,92 a 0,51 mg/l K^{+}, resp.) a anorganického dusíku (0,93 a 0,76 mg/l NH_4-N, resp.). Během vegetační sezóny se zvyšovalo pH a koncentrace rozpustného reaktivního fosforu (SRP), celkového P a NH_4-N v závislosti na klesající hladině podzemní vody. Na spáleništních plochách byly koncentrace SRP, celkového P a NH_4-N v půdní vodě až řádově vyšší než v blatkovém boru, koncentrace K^{+}, Mg^{2+} a Ca^{2+} byly cca dvakrát vyšší.

Vodní retenční kapacita subkontinentálního vrchoviště (lokalita Červené blato) se výrazně lišila během roku. Retenční kapacita závisí na aktuální hloubce hladiny podzemní vody. Je relativně vysoká v období se zakleslou hladinou podzemní vody (až cca 70 mm za týden). Naopak v období s vysokou hladinou podzemní vody (po vydatných deštích) byla retenční kapacita nízká a téměř všechna srážková voda odtékala z rašeliniště. Podobně, retenční kapacita pro dešťové srážky byla minimální mimo vegetační sezónu.

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INTRODUCTION

General

Peatlands are estimated to occupy roughly 500 million ha, or 3.8%, of the global land surface (Paavilainen et Päivänen 1995). Peatlands occur primarily in boreal regions where cold, waterlogged conditions promote accumulation of soil carbon (Gore 1983, Jeník et Soukupová 1989, Dierssen et Dierssen 2001). In central Europe, peatlands represent extrazonal ecosystems (sensu Jeník 1995) with a unique species composition similar to that in bogs of boreal regions (Spitzer et Jeník 2002). Whereas the northern peatlands form an extensive part of landscape with a strong influence on its energetic and material budget (e.g., Valentini et al. 2000, Vitt et Wieder 2006), the peatlands in central Europe represent mostly isolated islands within the zone of temperate forests with a rather marginal role in the whole landscape functioning. Nevertheless, isolated central European peatbogs are unique long-term habitat islands which have acted as palaeorefugia during the postglacial development (Nekola 1998). They enabled the long-term survival of relic boreal and subarctic species in the nemoral forest zone (relic insect species in Mikkola et Spitzer 1983, Spitzer et Jaroš 1993).

Extensive peatland complexes are found at two contrasting altitudes in central Europe. Firstly, peatlands are common at an altitude of about 1,000 m in precipitation-rich mountains, i.e., in montane altitudinal belts of the Šumava Mts., Krušné hory Mts., and Sudeten Mts., usually in contact with extrazonal coniferous taiga dominated by *Picea abies* (Spitzer et Jeník 2002). Secondly, several peatland complexes are found in lowlands and in the colline belt (South Bohemian Basins, Czech Cretaceous Basin, northern Poland and Germany) with rather flat macrorelief. Development and preservation of such peatlands are controlled mostly by local hydrogeological factors.

Peatlands are most fundamentally described by their hydrology. Ombrotrophic bogs depend solely upon precipitation for water and associated nutrients, whereas minerotrophic fens also receive varying amounts of ground- and/or surface-water inputs. These differences in water supply underlie large differences in soil chemistry, nutrient availability and plant species composition (Dierssen et Dierssen 2001, Chapin et al. 2004).

Open peatbogs are typical especially of Atlantic, precipitation-rich areas, whereas trees form an important part of the peatbog vegetation in northern, central and eastern Europe with lower precipitation. Specific types of raised bogs are found in these areas: (i) raised bogs with forested margins typical of boreo-subatlantic and boreo-subcontinental areas and (ii) so called treed or wooded peatbogs (Waldhochmoore sensu Neuhäusl 1972, lesní vrchoviště in Czech) in subcontinental and submontaneous areas.

Wooded peatbogs occur especially in north-eastern Europe affected by glaciation (Baltic region, E Scandinavia) with a rather continental climate (as. *Ledo-Sphagnetum magellanici* Sukopp 1959 emend. Neuhäusl 1969). Their typical feature is a flat or only slightly domed surface. The *Pinus rotundata*-dominated peatbogs can be regarded as their central European analogy.

Presence of trees in such peatbogs, especially of the *Pinus* genus, is considered as a natural phenomenon in continental climate with more or less pronounced dry summer periods. Water shortage restricts the growth of *Sphagnum* plants during summer, which in turn favours both the establishment and the growth of seedlings of trees and dwarf shrubs (Neuhäusl 1972). In general, tree growth is poor, largely due to inadequate aeration of the rooting zone caused by persistently high water table levels. Trees are of limited height (up to 10 m) and they form a rather sparse tree cover. Nevertheles, the established tree layer has a strong impact on: (i) the hydrology by intensive tree transpiration followed by water-level drawdown and (ii) radiation environment of the moss layer (increased shading). The survival of *Sphagnum* species may be threatened by both drying and shading by the established tree layer.

The aim of this chapter is to summarize available biological information about the bog pine forests. Emphasis is placed on their ecology and hydrology. However, there are many uncertainties associated with both nomenclatoric and syntaxonomical problems therefore other aspects, e.g., their syntaxonomy and taxonomical tasks regarding the dominant species are briefly touched on.

Pinus rotundata taxonomy

The group of taxa related to *Pinus mugo* TURRA has been revised in the recent literature several times (e.g., Christensen 1987, Farjon 1998, 2001, Businský 2008). However, the group shows still several taxonomic uncertainties associated with nomenclatoric problems (cf. Businský et Kirschner 2006).

In central Europe, the taxon usually called "bog pine" is frequently recognized (Moor-Spirke in German, blatka or borovice blatka in Czech, sosna blotna in Polish). The recent taxonomical studies by several Polish authors (Prus-Głowacki et al. 1998, Lewandowski et al. 2000, 2002, Boratyńska et Bobowitz 2001, Boratyńska et al. 2003, Boratyński et al. 2003, Boratyńska et Boratyński 2007) show that non-hybrid monocormic arborescent forms should be understood as a taxon separate from *Pinus mugo* s.str. Therefore, the Polish authors accept the bog pine as a separate species under the name *Pinus uliginosa* Neumann (Boratyński 1994). This taxon was interpreted similarly as a separate species in the last twenty years in the Czech botanical literature, but under the name *Pinus rotundata* Link. for the same taxon (Skalický 1988, Businský 1998, 2002). The name *Pinus rotundata* Link. was published as early as 1827. However, according to the study of Businský et Kirschner (2006), it should not be used as the correct name for the bog pine. Instead, the name *Pinus hartenbergiensis* Liebich should be used as the correct name at the rank of species.

Nevertheless, this monocormic arborescent form was not always recognized as an entity distinct from the prostrate frutescent form within the *Pinus mugo* complex (e.g., Holubičková 1965, 1980), especially in areas with the presence of intermediates between *P. uncinata* subsp. *uncinata* and *Pinus rotundata* (e.g., West Germany).

Nowadays, Businský (2009) made an extensive study of natural populations of the *Pinus mugo* complex throughout its distribution range from E Spain to the Balkans. The author formed a new taxonomic and biogeographic concept of the bog pine according to his newest results. He described the bog pine as a subendemic species for the Czech Republic with several overlapping occurrences at a maximum distance of 25–30 km from the Bohemian frontier, for which he accepted the name *Pinus uncinata* subsp. *uliginosa*. This new combination [*Pinus uncinata* RAMOND ex DC. subsp. *uliginosa* (Neumann) Businský comb. nova] was proposed by Businský et Kirschner (2006).

This taxonomically complicated group of pines represents probably evolutionarily young taxa that hybridize intensely with one another. Even fertile hybrids with *Pinus sylvestris* L. were found. The interspecific hybrid combination *P. rotundata* × *P. sylvestris* (= *P.* × *digenea* Beck.) occurs commonly in the Třeboň Basin; therefore introgressive hybrid populations are found there at most localities (Businský 1998).

However, up to now no complex molecular study has been published which could resolve these taxonomical tasks. Therefore, throughout this ecological study we follow the concept of Skalický (1988) and Businský (1998) according to which three separate species are distinguished: *Pinus mugo*, *P. uncinata* and *P. rotundata*, each of them with relatively clear morphological, geographical and ecological differentiation. *Pinus mugo* has a typical prostrate form, and usually occurs in the subalpine belt in central and SE Europe. *Pinus uncinata* has an arborescent form and usually occurs in the mountain ranges of W Europe (Alps, Pyrenees). *Pinus rotundata* has the same arborescent form, it is the most specialized species occurring only in the submontaneous peatbogs of central Europe.

Distribution of *Pinus rotundata*

Bog pine has only a limited geographical distribution in central Europe (Fig. 1) which includes parts of Germany, Austria, Poland and the Czech Republic (Jalas and Suominen 1973). The centre of its distribution is in the southwestern and the southern part of the Czech Republic. The typical arborescent form occurs only in submontaneous peatbogs, at higher altitudes it forms introgressive hybrids with *P. mugo* of a rather prostrate form (Businský 1998, Skalický 1988). However, in the most recent study of Businský (2009), the bog pine is described as a subendemic species for the Czech Republic with several overlapping occurrences at a maximum distance of 25–30 km from the Bohemian frontier.

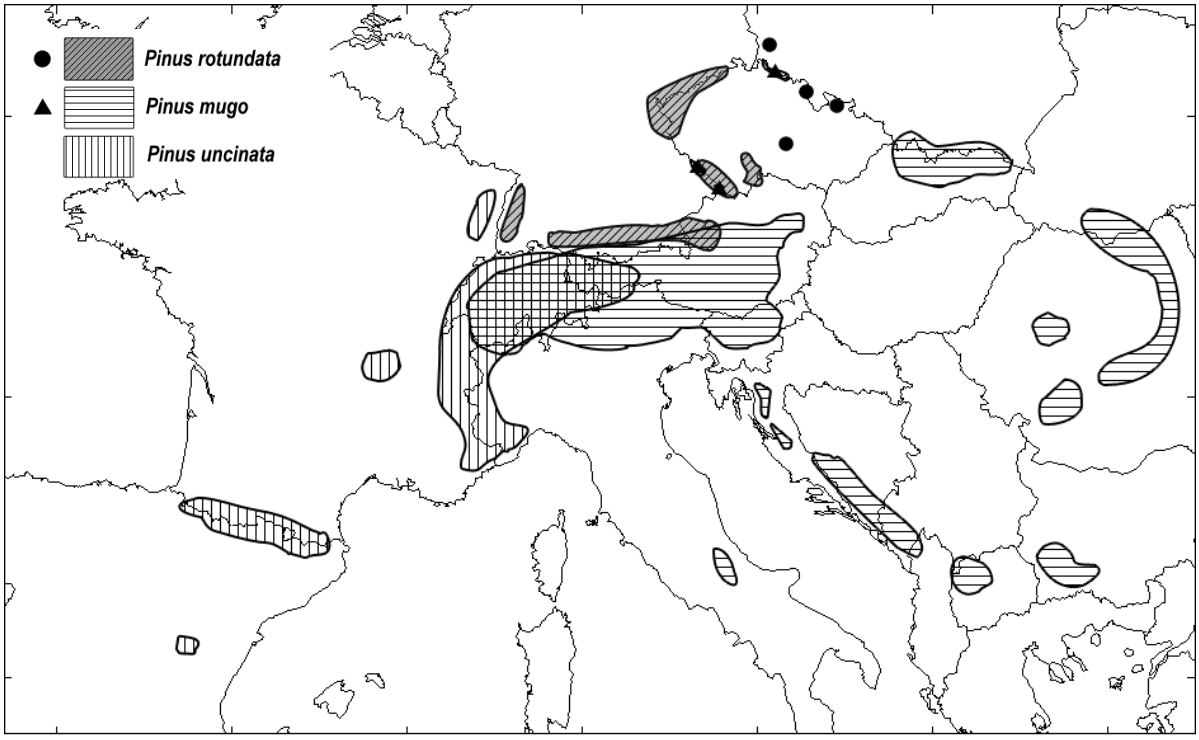

Fig. 1. Geographical range of *Pinus rotundata, P. uncinata* and *P. mugo*. Orig. in Bastl et al. (2008), modified from Jalas and Suominen (1973).

The biology and ecophysiology of *Pinus rotundata*

There are only few studies devoted to the biology or physiology of *Pinus rotundata* (von Sengbusch 2004, Mach 2007, Bastl 2008). Instead, most studies concern taxonomical problems (e.g., Businský et Kirschner 2006, Boratynska et Boratynski 2007, for others see previous paragraphs), syntaxonomy and vegetation description (e.g., Neuhäusl 1972, Neuhäusl 1984, Navrátilová et al. 2006, Bastl et al. 2008), vegetation changes and succession (Neuhäusl 1992, Rektoris et al. 1997, Horn et Bastl 2000, Kučerová et al. 2000, Frelechoux et al. 2000a, Frelechoux et al. 2003, Rektoris et al. 2003, Frelechoux et al. 2004, Bastl et al. 2009), paleoecology (Jankovská 1980, Rosch 2000, Mitchell et al. 2001, Svobodová et al. 2002) or growth dynamics and dendrology (Musil 1968, Brang 1988, Frelechoux et al. 2000b, Soukupová et al. 2002).

P. rotundata reproduces only by seeds. Seeds have a relatively good germination capacity and the seedlings have high vitality (Bastl 2008). However, *Pinus rotundata* is a relatively light demanding species, therefore canopy openness is probably crucial for its reproduction (Schmid et al. 1995, von Sengbusch 2004). During the last decades the germination of bog pine has been supressed by the dense shrub layer in most localities. Ecology of *Pinus rotundata* seedlings, and partly also of the accompanying trees *Pinus sylvestris* and *Picea abies*, was studied by Mach (2007), Mach et al. (2009) and Bastl (2008). Requirements of *Pinus rotundata*, in comparison to the co-occurring tree species *Pinus sylvestris* and *Picea abies*, were studied in relation to groundwater, light and nutrient supply by Bastl (2008). The experiments showed that a high groundwater table would probably favour seedlings of *P. rotundata* compared to *P. sylvestris* and *P. abies*. Added nutrients enhanced the growth of all three species. Additionally, *P. sylvestris* seedlings showed higher resistance to dryness than those of *P. rotundata* (Mach 2007).

Pinus rotundata height is usually well correlated with water table depth probably through the concentration of oxygen in soil water and in soil pores (von Sengbusch 2004). The maximum height of *P. rotundata* is 20 m according to Skalický (1988) in drained peatbogs. Its maximum height is usually up to 10 m in pristine bogs.

The species has probably only a limited opportunity to sustain severe frosts as reported, e.g., by Soukupová et al. (2002). They found a depression of growth increments in years with severe winters with hard frosts (1898-1901, 1940-1946), especially in waterlogged soils with a loose canopy in the Libořezy peatbog.

Depression of growth increment were also reported for periods of droughts on the inclined bog margins with a closed bog pine canopy (Soukupová et al. 2002). According to Bíba et Kaňák (2000) the radial growth is more regular in *Pinus rotundata* compared to that of *Pinus sylvestris* on the same sites in the Losí blato peatbog. The radial growth declined rapidly in both pines around the age of 20 years, probably as a reaction to limited development of the root system due to high water table. Therefore, the root system is usually very shallow (according to the mean water table) making the tree susceptible to frequent windbreaks.

Surprisingly, there are several *P. rotundata* plantations on mineral soil (mainly acidic sand) where the species grows successfully. The species may have a broader ecological amplitude but only in the case of low competition and optimum light conditions. Therefore *P. rotundata* may be described as a tree of a broader environmental range yet of an exceptional tolerance of waterlogged soils (e.g., von Sengbush 2004, Bastl 2008, Kučerová et al. 2010a).

The only information about the transpiration of *Pinus rotundata* was given by Neuhäusl (1975). In his study, the transpiration was measured during one hot summer day (24 h) by Ivanov´s gravimetric method, i.e., by the short-term weighting of needles. The transpiration of *P. rotundata* was lower than that of *P. sylvestris*, in both species no midday depression of transpiration was detected.

Some specific characteristics of water relations could be derived from several transpiration studies made on *P. sylvestris* which belongs to the most studied tree species in Europe (e.g., Vincke et Thiry 2008, Verbeeck et al. 2007, Irvine et al. 1998) – generally speaking, in response to soil water deficit, mature Scots pine closes its stomata sufficiently to prevent the development of substantial xylem embolism (Irvine et al. 1998, Zweifel et al. 2007). However, even if the soil is sufficiently wet, leaf conductance decreased with increases in vapor pressure deficit above 1 kPa (as measured in the Hartheim *Pinus sylvestris* plantation on the Upper Rhein Plain, Germany, by Sturm et al. 1998).

Bog pine-dominated peatbogs – their characteristics and distribution

So called "bog pine peatbogs" (blatková vrchoviště in Czech) are suppossed to be a final stage of raised bog development in submontaneous areas (Neuhäusl 1972). According to Oberdorfer (1992) they represent a subarctic-alpine relic community from the Late Glacial Period, which survived the expansion of forest vegetation in peatlands during the Holocene.

Besides the bog pine, also other tree species form the tree layer such as Scots pine (*Pinus sylvestris*), or its hybrid with bog pine (*Pinus* × *digenea*), Norway spruce (*Picea abies*) or birch (*Betula pubescens* or less often *Betula pendula*) (Kučerová et al. 2001). The tree layer may have different height and density. Tree height is usually 8–10 m, whereas it can reach up to 18 m in peatbogs affected by moderately drainage. Tree density can range from individual scattered trees to closed forest stands. The ground layer is usually sparse. Dwarf shrubs such as *Ledum palustre, Oxycoccus palustris, Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea* dominate here, whereas *Eriophorum vaginatum* and mosses (*Sphagnum* sp.) dominate at wetter sites. In the moss layer, the peat mosses prevail (*Sphagnum capillifolium*, *S. fallax*, *S. flexuosum, S. magellanicum* , etc.), while other moss species are more common in drier parts (e.g., *Dicranum polysetum, Hylocomium splendens, Pleurozium schreberi*, *Polytrichum strictum*) along with the lichens (*Cladonia* sp.).

The centre of the distribution of bog pine-dominated peatbogs lies in the submontaneous and montaneous altitudes of the Sudeten-Hercynian Mts. In this area, such a vegetation is considered as a climax vegetation on rather deep peat sediments (Neuhäusl 1992). Naturally, their occurrence is limited to the areas with the occurrence of *Pinus rotundata* nevertheless communities with a very similar species composition were documented also from the Vogesen Mts. where *P. rotundata* is naturally absent (Kaule 1974, Bick 1986, so called treeless variant).

Several localities are documented from southern Schwarzwald (Dierssen et Dierssen 1984), where more continental species such as *Ledum palustre* are absent. Other localities are found in the Schweizer Jura (Freléchoux et al. 2000a,b), in Bavarian foothills of the Alps, Fichtelgebirge, Oberpfälzer Mittelland and Bayerischer Wald (Lutz 1956, Wagner et al. 1997), futhermore in the Waldviertel area (Steiner 1992) and in south-western Poland (e.g., Góry Bystrzyckie (Torfowisko pod Zieleńcem), Góry Stołowe (Wielkie Torfowisko Batorowskie) and Bory Dolnoślaskie (Torfowisko pod Węglińcem, Staszkiewicz et Tyszkiewicz (1972)). Additionally, *P. rotundata* was planted in the Hautes Vosges (Alsace, France) by German forest managers prior to 1914 (Begeot and Richard 1996).

In the Czech Republic, the bog pine-dominated peatbogs occur especially in the southern and south-western parts of the country (Fig. 2), Třeboň Basin, lower altitudes of the Šumava Mts., Český Les and Slavkovský Les Mts.), several localities are found also in the Krušné hory Mts., only discrete localities are documented from the Žďárské vrchy (Dářko) and Hrubý Jeseník (Rejvíz, secondarily the Skřítek peatbog). The complete list of recent localities is given by Businský (1998, 2009).

Syntaxonomy of bog pine dominated peatbogs

The syntaxonomy of bog pine peatbogs was studied by Neuhäusl (1972, 1984) and more recently by Navrátilová et al. (2006). In the Czech phytocoenological literature the bog pine stands are usually evaluated as the broad *Pino rotundatae-Sphagnetum* association following the concept of Neuhäusl (1972, 1984). He ranged all stands with bog pine inside this association regardless of the tree and moss cover. He distinguished the stands with different moss or tree cover only as different subassociations (e.g. *sphagnetosum, ledetosum, vaccinietosum*).

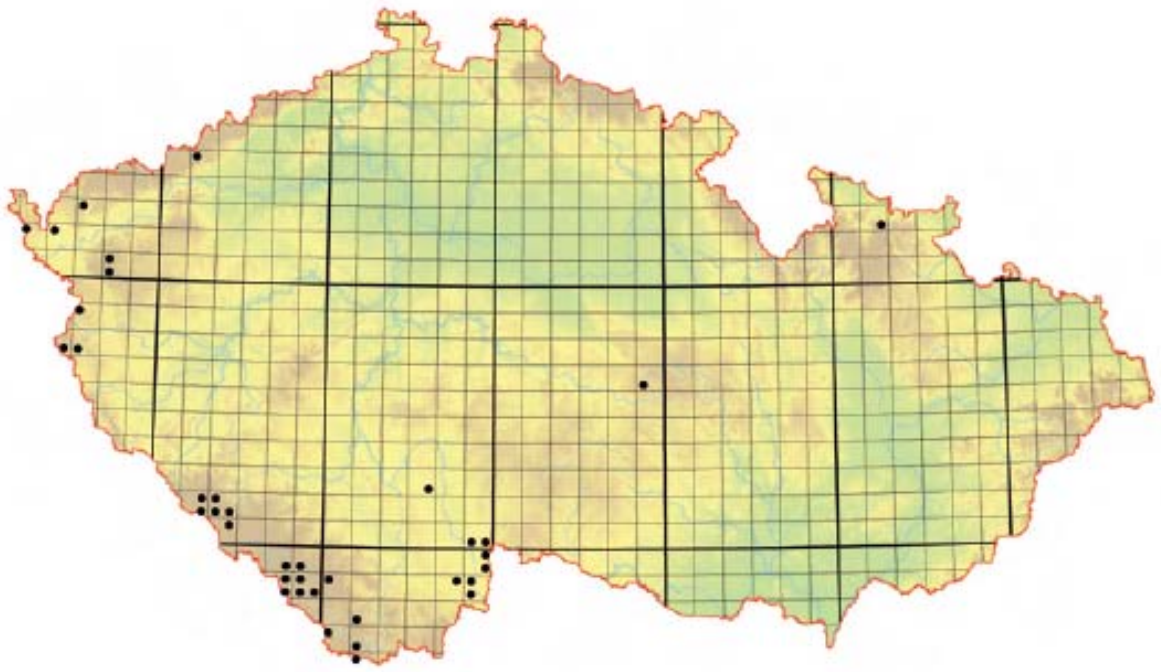

Fig. 2. The map of the recent distribution of the biotop "L10.4 Blatkové bory" in the Czech Republic (orig. in Kučerová et al. 2010b).

In contrary, the concept of this association is narrower in the German phytocoenological literature. Oberdorfer (1992) ranged only the open bog pine stands into the *Pino rotundatae-Sphagnetum* ass. (Kästn. et Flöss. 1933) Neuhäusl 1969 (class *Oxycocco-Sphagnetea* Br.-Bl. et Tx. 1943). These stands represent the initial and optimal succesional stages of the community development (analogous to the subass. *sphagnetosum* a *ledetosum* according to Neuhäusl 1972), sometimes they have been ranged also as the *Sphagnetum magellanici pinetosum rotundatae* subass. (Oberdorfer 1992). The final succesional stages of the closed bog pine forest (analogous to the *vaccinietosum* subass.) have been ranged as the *Vaccinio uliginosi-Pinetum rotundatae* association, Oberd. 1934 emend. Seibert in Oberd. 1992 (class *Vaccinio-Picetea* Br.-Bl. in Br.-Bl. et al. 1939). This association comprises only final, usually degradated succesional stages of the bog pine forest after the drainage. This association was refered especially from Germany (e.g. in Schwarzwald Mts. by Oberdorfer 1992 and von Sengbush et Bogenrieder 1998, in Schweizer Jura by Freléchoux et al. 2000a, b).

However, Dierssen et Dierssen (2001) adopted quite different approach in their summary about central European peatbogs. Due to still very unclear taxonomy of *Pinus mugo* complex they evaluated all communities with both *Pinus rotundata* and *Pinus mugo* str. as the broad *Pino mugo-Sphagnetum magellanici* association.

More recently, Navrátilová et al. (2006) have tried to re-define commonly used vegetation units of pine dominated bog forests in a formal way based on combination of different species groups. Analysis of relevés from the Czech National Phytocenological Database was carried out. The results showed that the communities are only fuzzy delimited with several transitions. Such situation probably mirrors the successional interconnection among different

associations (Neuhäusl 1992, Oberdorfer 1992). Therefore, the vegetation of the bog pine dominated peatbogs was divided in two communities of two different classes, according to their succession, similarly to the stands with dominant *Pinus sylvestris*. The beginning and optimal successional stages were categorized as *Pino rotundatae-Sphagnetum* community (*Oxycocco-Sphagnetea* class, *Sphagnion medii* alliance) whereas the final successional stages with several species from the *Vaccinio-Piceetea* class were recognized as *Vaccinio uliginosi-Pinetum rotundatae* community (*Vaccinio-Piceetea* class, *Dicrano-Pinion* alliance). In later community the tree layer is higher, chamaephytes dominate in the herb layer. In the moss layer several typical forest mooses occur (e.g. *Pleurozium schreberi, Dicranum scoparium*) along with the *Sphagnum* sp. Usually the stands were influenced by drainage in the past. The stands with dominant *Pinus mugo* str. or *P.* × *pseudopumilio* was recognized as a separate community (as. *Pino mugo-Sphagnetum* in *Oxycocco-Sphagnetea* class). Even if the species composition is partly similar with previous communities, the *Pino mugo-Sphagnetum* community has quite different physiognomy and ecological requirements (Bastl et al. 2008). Concept of Navrátilová et al. (2006) was followed throughout this study.

Only rarely minerotrophic bog pine dominated stands was reported in literature, e.g., from Bavaria (Wagner et al. 1997) and in several relevés from the Příbrazské peatbog (Třeboň Basin, Holubičková 1960). Typically, the stands are formed by both bog and fen characteristic species (e.g., *Carex lasiocarpa, C. rostrata, C. nigra, Menyanthes trifoliata, Equisetum fluviatile, Eriophorum angustifolium, Sphagnum warnstorfii*), the tree layer is rather open. There are several microhabitats with quite different recharge of water (minerotrophic hollows x oligotrophic hummocks). Wagner et al. (l.c.) classified them as a separate *Carex lasiocarpa-Pinus rotundata* community with broad ecological amplitude (pH 4,2-6,5, conductivity 10-250 $\mu S.cm^{-1}$) and species composition similar to the *Caricion lasiocarpae* alliance. Some of these stands could probably develop as a result of spontaneous colonisation of *Pinus rotundata* in abandoned sedge peaty meadows in the second part of the 20th century (e.g., in the Alp foothills). Others may develop in specific hydrological situations such as in ombrosoligenous sloping bogs with numerous natural springs or in peatbog margins with adjacent mineral slope (Holubičková 1960). The great vitality of bog pine in such stands suggests of broader ecological amplitude of this species then usually suppossed from the contemporary species occurrence mostly in oligotrophic peatbogs.

The ecology of *Pinus rotundata* dominated peatbogs, limiting factors

Pinus rotundata-dominated peatbogs are usually found in peatbogs fed mostly by precipitation, that are more than two metres deep and of slightly convex shape. In undisturbed habitats the groundwater table (GWT) does not usually drop beyond 30 cm below the soil surface. However, Neuhäusl (1972) supposed that the community is not purely ombrotrophic and that it can be partially saturated with oligotrophic water from mineral bedrock.

The competition between the trees and the moss layer is a typical feature of wooded peatbogs in general (pines contra sphagna). The growth and long-term survival of trees is possible only in areas with rather dry summer periods. In those periods, *Sphagnum* growth is limited due to lower water saturation, making suitable conditions for the growth of tree seedlings. Survival of *Sphagnum* species may be threatened by both drying and shading by the established tree cover. Against expectations, the *Sphagnum* species, found only in open habitats, had a lower photosynthetic capacity and maximum quantum yield than those growing in half-shade (Hájek et al. 2009). Therefore the dominant sphagna probably can grow better in partly shaded wooded peatbogs with only scattered trees than species in the open

pristine peatbogs, especially in a subcontinental climate with rather hot and dry summers connected with long-term stressful conditions of full light.

The other typical feature is a cyclic, small-scale tree layer regeneration in relation to natural changes of water regime. Lower summer precipitation = higher cover of trees = higher evapotranspiration = pronounced drop of groundwater table = lower cover of moss layer = higher cover of ericoid shrubs. However, after an abrupt breakup of the tree layer, e.g., as a result of senescence = lower evapotranspiration = rise of water table = increased moss cover. Both continuous tree regeneration and small-scale breakup of the tree layer are common especially in natural stands.

Not only the mosses but also the trees follow tightly the changes in water régime – both their cover and increments increase rapidly as a result of drainage; on the other hand the tree layer breaks up rapidly in the case of abrupt water table elevation (e.g., during restoration, exceptionally flooding or wetter periods, e.g., Schweingruber 1996).

The recent occurrence of *Pinus rotundata*-dominated bog forests seems to be determined by several factors:

1. Holocene history – the *Pinus rotundata*-dominated bog forests are probably limited to the areas of glacial refuge of this endemic species or to their broad surroundings. Communities similar to the recent *Pino rotundatae-Sphagnetum magellanici* are found starting from the young Atlantic period in the Třeboň peatbogs according to Jankovská (1978). In that time, the species had only very limited possibility to disperse from distant glacial refuges through dense Atlantic forests. Instead, the species could be present much earlier in the same peatbogs probably as small patches or as isolated individuals in the surroundings.
2. Altitude – Bastl et al. (2008) studied the vegetation of the *Pinus rotundata*-dominated peatbogs on a broad altitudinal gradient (470-1210 m a.s.l.). The growth form of the dominant species (tree-like *P. rotundata* contra shrub-like *P.* × *pseudopumilio*) was closely associated with altitude. They also found close association with altitude in several environmental factors including pH, electrical conductivity, soil moisture content and temperature amplitude.
3. Climatic conditions – The subcontinental or continental character of the climate with rather dry summer periods is crucial for the reproduction of the species. In such periods the *Sphagnum* growth is limited due to lower water saturation, creating suitable conditions for the growth of tree seedlings in the still moist *Sphagnum* carpet (Neuhäusl 1972). The other important factor can be the rather limited snow cover during winter. Even low snow cover (20-40 cm) in the Třeboň Basin can influence the growth form of several peatbogs species – young stems of birches and pines may be inflected by the weight of heavy snow, sometimes they can be broken, small stems of ericoid shrubs are pressed down into the *Sphagnum* carpet. In the central part of the Šumava Mts. with rather high snow cover (>1m), the peatbogs are colonised by shrub-like *Pinus* × *pseudopumilio* which may be better preadapted to high snow cover. Similarly we could find only *Pinus mugo* str. at higher altitudes of the northern Schwarzwald Mts., Krkonoše Mts., etc., with high snow cover during winter.
4. Soil properties and water quality – *P. rotundata*-dominated peatbogs usually occur on quite deep peat (more than 2 m). Therefore we can suppose no or only limited recharge of water from the mineral bedrock. The soil water is usually very acid and poor in base cations. However, such a limitation can be influenced by the distribution of the species since the early Holocene – the species has been able to survive only in the oldest peatbogs (with the deepest peat in recent time), see a).
5. Human impact – Several localities were destroyed by drainage, forest plantations, peat extraction or reservoir construction (Lipno reservoir). On the other hand, the drainage made at the beginning of the 19th century on several peatbogs in the Třeboň Basin had

accelerated the successional shift from the open peatbog vegetation (*Sphagnion medii*) with only scattered trees towards denser *Pinus rotundata*-dominated bog forests. Similarly, Begeot and Richard (1996) conclude that the recent increase in *P. rotundata* in peatbogs in the Schweizer Jura is a consequence of drainage and peat extraction. The recent abundance of *P. rotundata* in the undisturbed Praz-Rodet bog (Schweizer Jura) was probably induced by clearance of the forest on mineral soil around the bog (Mitchell et al. 2001). The forest had functioned as a windbreak reducing evapotranspiration in this small bog. When the protection disappeared, the mesoclimate was altered and the bog became more dried.

Peatbogs in the Třeboň Basin

Complexes of oligotrophic peatlands (bogs), minerotrophic peatlands (fens) and adjacent wooded swamps cover about 17,000 ha of the Třeboň Basin Biosphere Reserve (Spitzer and Jeník 2002). Occurrence of the Třeboň mires at temperate mid-latitude and subcontinental longitude in the colline/submontane belt, makes them a fairly unique biogeographical "archipelago" of ecological islands in central Europe (Spitzer and Jeník 2002).

The occurrence of numerous peatbogs is enabled by suitable hydrogeological conditions of the area, especially by bad drainage conditions in a tectonic basin, high regional groundwater table, several flushes of artesian waters and by a high representation of clayish soils creating watertight layers (Jeník et Přibáň 1990). Most peatbogs are topogenic formations originating on sites flooded locally by groundwater which drains along stratigraphic faults to the surface (Procházková 1978). A variety of peatlands developed as open peatbogs, wooded peatbogs, acidic fens, sedge- and grass-dominated wetlands and willow and alder carrs according to the amount and stability of upwelling water and amount of available nutrients (Květ et Jeník 2002). A specific type of mires developed in close vicinity of numerous fishponds, which are partly saturated by surface water (subsurface inflow from fishponds). Their vegetation-environment relationships and vegetation changes during last 50 years were investigated by Navrátilová (2006).

Bog pine dominated peatbogs in the Třeboň Basin

Historical development

Most of deep peat sediments in the Třeboň Basin have developed since the Early Holocene, especially in the central part of the basin, including the recent *Pinus rotundata* dominated peatbogs (Jankovská 1978, 1980). Shallow water bodies, mesotrophic sedges or reeds were the first peat accummulating vegetation. Species typical of oligotrophic mires have occurred there since the Atlantic period (e.g., *Sphagnum* sp., *Eriophorum vaginatum*, *Oxyccocus palustris* , etc.). *Ledum palustre* and probably also *P. rotundata* could occur in that time forming typical bog pine woodlands at the beginning of the Subatlanticum.

Available evidence (only moderately decomposed sphagnum peat in places where the closed bog pine forest are present nowadays, pers.observ.) indicate that original bog pine-dominated peatbogs were probably only slightly domed, their central parts were wetter, rather open, only with scattered stunted *Pinus rotundata* trees (up to 4–6 m tall). In the uderstorey *Sphagnum* species, *Eriophorum vaginatum* and dwarf shrubs dominated (Jankovská 1980). Higher tree densities were limited only to the peatbog margins. Similar vegetation can still be found in some localities in the Šumava Mts. (e.g., Hůrecká slať, Velká Niva). Such vegetation zonation was probably preserved until the first human impact at the end of the 18th century.

Even small changes in water balance, induced by artificial drainage, strongly affected the former vegetation zonation. Both tree height and their radial increments were supported by

the drainage. The survival of bog pine seedlings increased whereas the heliophil species such as *Andromeda polifolia, Oxycoccus palustris* or *Sphagnum* sp. retreated as a result of increasing shading and lower water table. Thus the present vigorous *Pinus rotundata* stands as found in almost all localities of *P. rotundata* may be regarded as a man-made artefact.

Description of localities

The total area of bog-pine dominated woodlands was probably more than 600 ha in the 1850s´ according to Ambrož (1948) whereas it declined to 457 ha in 1989 (Plíva et Žlábek 1989). Nowadays, only five peatlands of the Třeboň Basin are dominated by old-growth stands of bog pine (Fig. 3):

- Červené Blato bog – the first study site, was influenced by drainage at the beginning of 19th century and by peat digging (cca 1860-1910). Nowadays, it represents the best preserved bog pine-dominated woodland in the Třeboň Basin with the largest population of *Pinus rotundata* and *Ledum palustre* (Rektoris 1994, Jeník et al. 2002). The occurrence of several relic insect species was documented by Spitzer et Jaroš (1993).
- Žofinka bog – the second study site represented the best preserved bog pine-dominated woodlands until the 1980s´ (Kučera 1977, Liška et al. 1989). Large-scale dieback of *Pinus rotundata* in both localities since the 1980s´(e.g., Kloubec 1995, Rektoris et al. 1997) was the main stimulus for investigations of their vegetation and hydrology (Kučerová et al. 2000).
- Borkovická blata peatbogs (N part) was the most extensive locality in the northern part of the Třeboň Basin. Unfortunately, most stands were completely extracted during the second part of 20th century and only a marginal strip of bog pine-dominated woodland was preserved as a reserve (91 ha). However, this fragment is also negativelly influenced by drainage. *Pinus rotundata* has stepwise retreated – there is a high proportion of hybrids (*Pinus* × *digenea*), high admixture of *Betula* sp., *Picea abies* and *Pinus sylvestris. Pinus rotundata* seedlings are very rare there.
- Libořezy Bog –remained undisturbed until the beginning of the 1980´s when the locality was licensed for peat extraction. Recently only a small part of this mire complex was designated as the Losí Blato Nature Reserve. A detailed vegetation study was made by Soukupová et al. (2002) in 1983, prior to the irreversible destruction of the locality. It described the whole vegetation zonation from a treeles zone of the *Eriophoro vaginati-Sphagnetum recurvi* ass. through bog pine woodland (*Pino rotundatate-Sphagnetum* ass.) towards the spruce-dominated lagg zone along the gradient of surface waterlogging and decreasing depth of peat.
- Široké blato Bog – situated on the Czech–Austrian border, has remained mostly untouched and was declared a nature reserve in 1994.

The rests of *P. rotundata* stands occur also in a peatbog in the vicinity of the Červené blato peatbog (Kočičí blato) which has been almost completely destroyed by peat extraction. There is only limited opportunity to discover all former localities of bog-pine dominated peatbogs in the Třeboň Basin (cf. Ambrož 1927). In the past, *P. rotundata* could grow also in more minerotrophic peatbogs, similarly to some peatbogs in Bavaria (Wagner et al. 1997). In the Borkovická blata peatbog Vilhelm (1901) reported the occurrence of *P. rotundata* along with *Sphagnum* sp., *Vaccinium uliginosum, Ledum palustre*, but also with more nutrient demanding species such as *Carex lasiocarpa, Salix aurita, S. pentandra* and *Eriophorum angustifolium*. Similarly Vilhelm (l.c.) documented *P. rotundata* along with *Equisetum limosum, Menyanthes trifoliata* and *Salix aurita* from the extinct peatbog in the vicinity of Třeboň (sv. Vít). Additionaly many peaty forests (e.g., in the forest district of Barbora, Cep or

Zámecký revír) were drained and planted already at the beginning of the 19th century. Unfortunately, we have no evidence of their former vegetation.

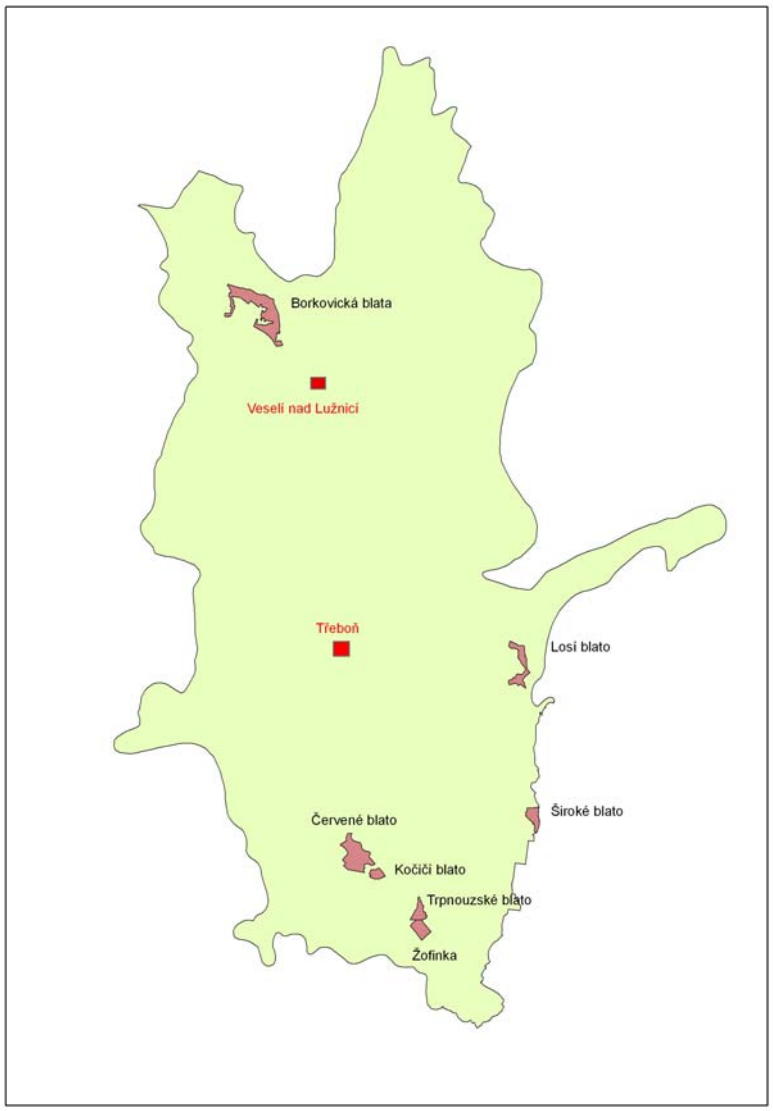

Fig. 3. Recent localities of the *Pinus rotundata* dominated peatbogs in the Třeboň Basin, Czech Republic.
Orig. L.Rektoris.

Human impact

Many *Pinus rotundata* populations have been destroyed in the Czech Republic as a consequence of peatland drainage, peat digging and peatland afforestation during the last 200 years. An extreme example was the total devastation of a large *P. rotundata* population during the construction of the Lipno water reservoir in the 1950´s. First references of drainage and peat digging were recorded in the Třeboň Basin from the end of 18th century (Spirhanzl 1951). Even the peatbogs not directly used for peat digging were human-affected, especially by the construction of drainage ditches along peatbog margins. The main reason was to protect the neighbouring forests from waterlogging and to increase timber production.

Almost all peatbogs found in the Třeboň Basin have been affected by drainage or peat extraction during the last 200 years (about 90% of the 7,680 ha of bogs, Spitzer and Jeník 2002). In some peatbogs (e.g., Červené blato and Borkovická blata peatbogs) this drainage has accelerated the successional shift from the open peatbog vegetation (*Sphagnion medii*) with only scattered trees towards denser *P. rotundata*-dominated bog forests, seen, e.g., along the nature trail through the Červené blato peatbog. Additionally, frequent hybridization with *P. sylvestris* is the next serious threat to the population survival, especially at the lower altitudes (Businský 1998). The expansion of *Pinus sylvestris* is further supported by the common forestry practice (forest plantations). Therefore, *Pinus rotundata* is considered as a critically endangered species because of the long-term disturbations of its environment and population isolation.

Water balance of a peatbog

Hydrologically, mires can be divided into two categories according to the nature of their water supply. Fens are mires developing in valleys or topographic basins. Part of their water recharge comes from precipitation, but they also receive varying amount of groud- and/or surface water. Most bogs, by contrast, are recharged mainly by precipitation, therefore surface vegetation in their central parts is largely isolated from the influence of the groud- and/or surface water (Ingram 1983).
The general water balance equation can be expressed as:

$$P + N – D – E – \Delta W - \eta = 0 \qquad (1)$$

Here: P = precipitation, N = total surface and sub-surface recharge, D = total surface and sub-surface discharge, E = evapotranspiration, ΔW = stored water and η = error term.
The water balance and the water table dynamics of a given peatbog are therefore the results of several terms: (i) climate (i.e., precipitation, radiation and temperature), (ii) recharge, (iii) soil physical features, (iv) discharge, and (v) evapotranspiration mediated via vegetation composition.

(i) Climate – there are important general correlations between mire distribution and precipitation, with fens predominating in areas of low rainfall, raised bogs in wetter conditions, and blanket mires in the wettest parts. Indeed it is clear that variation in evaporation (given by temperature and radiation) strongly modifies the geographical effect of precipitation on mires. For example, in temperate regions evaporation often decreases with altitude as cloudiness increases and radiation diminishes. Also, the form of precipitation can profoundly affect mire development. The total amount of snow could affect the distribution of chionophobous or chionophilous vegetation types as shown, e.g., by Sonesson (1970) for northern Sweden.

(ii) Recharge term is traditionally suppossed to be almost zero in the case of central parts of bogs (so called mire expanse). However, sub-surface recharge can form a substantial part of the water input into the bog slope and laggs, additional recharge from mineral bedrock can contribute to the water balance of deeper peat layers. Unfortunately reliable data about the amount of such recharge are scarcely. Even in fens the recharge term is measured only exceptionally.

(iii) The properties of surface peat horizons differ greatly from those of the permanently anaerobic deeper peat. Ingram (1978) introduced the terms acrotelm and catotelm for the surface and lower horizons, respectively. The thickness of the acrotelm varies from over 50 cm in many hummocks to less than 10 cm in hollows (Damman 1986). In actively growing raised bogs, the acrotelm is formed by porous peat with high hydraulic conductivity while the catotelm is formed by compacted peat, saturated with water and being practically impermeable (Ivanov 1975). Therefore the water table mound is formed in a raised bog as described by the traditional hydrological model (Ingram 1983). Precipitation infiltrates into the uppermost layer of porous peat (acrotelm) and then flows laterally toward the bog margins because deeper infiltration is blocked by the low hydraulic conductivity of the deeper peat (catotelm).

(iv) There are two main forms of water output from a mire – output in the form of liquid water and water vapour. Discharge in the form of vapour is discussed in detail in the next section. Several water discharge processes operate in mires such as infiltration flow (or seepage = mass transport of water through porous media), pipe flow (belowground discharge through systems of tunnels, typical esp. of blanket bogs and reviewed broadly by Ingram (1983)), overland flow (in mires important only in exceptional situations, e.g., during floods), and open channel flow which is very often altered by human activities (surface drainage). The extensive review of water discharge processes is given by Ingram (1983). Both discharge and recharge processes are modified to a large extent by the morphology of a peatbog and both can substantially change during the ontogenesis of a given peatbog. Diagrammatic classification of recharge, throughflow and discharge processes during the initial and final phases of development of various types of mires was given, e.g., by Ivanov (1953, 1975).

(v) Evapotranspiration (ET) is the principal component of water discharge from a mire. The magnitude of the ET flux is controlled at any moment by the energy available, by the ability of the atmosphere to take up the evaporated moisture and finally by the water supply. Especially the water supply can be modified to a large extent by the vegetation itself. Hummock-forming *Sphagnum* species have pendent branches that are tightly appressed to their stems, which effectively transport water by capillary suction to the surface (Rydin 1985). Moreover, *Sphagnum* leaves have a large surface area and are composed of numerous porous, dead hyaline cells that can store large amounts of water (Clymo and Hayward 1982). However, the capillary rise is unable to sustain the supply of water to the surface of a *Sphagnum* cushion under strongly evaporative conditions (Overbeck and Happach 1957, Neuhäusl 1975, Ingram 1983) even when the water table is high. Instead, the evaporation from the *Sphagnum* cushion can be very limited under such conditions and the surface of the *Sphagnum* carpet displays temperature fluctuations of a great amplitude, as reported, e.g., by Neuhäusl (1975) or more recently by Hojdová et al. (2005). By contrast, dwarf shrubs and graminoids, both of which form a characteristic part of the peatbog vegetation, have roots and vascular systems which can effectively absorb groundwater. Therefore these plants can transpire more intensily also during strongly evaporative conditions. Nevertheless, a high proportion of peatbog plants show, to some degree, xerophytic or xeromorphic features (e.g., evergreenness, small leaf surface area, highly revolute leaf margins) designed to reduce transpiration (Ellenberg 1996). Their possibly intensive transpiration was notoriously speculated by several authors (e.g., Firbas 1931, Small 1972). According to studies of Small

(1972), these plants are able to transpire at a similar rate as mesotrophic species of a similar standing biomass. Their xeromorphic character was therefore explained as a result of low availability of nitrogen in peaty soil and consequently by low contents of nitrogen in their leaves and stems (Müller-Stoll 1947). Usually, their transpiration is primarilly controlled by direct reaction of stomata to increasing leaf to air vapour pressure deficit rather than by decline of leaf water potential (Kolmanová 1997).

Different types of vegetation can influence also the seasonal dynamics of water uptake from the soil (Ingram 1983). Mosses, for example, are able to evaporate water during the whole year in relation to the atmospheric conditions (temperature, humidity) and their water saturation whereas both deciduous and evergreen vascular plants can transpire only during the main growing season.

The ET is additionally influenced by (i) total aboveground biomass and (ii) vegetation height (different aerodynamic surface roughness – the taller a plant is = rougher surface = faster transport of water vapour from the leaf surface = faster transpiration). Therefore, the stands consisting of trees with both relatively high biomass and height should have higher transpiration than stands with low stature vegetation such as *Eriophorum*-dominated stands or stands with an extensive *Sphagnum* cover.

Despite an abundance of water and nonvascular vegetation, ET in peatlands is generally less than open water ET. In peatlands with an abundance of vascular plants, there is evidence that ET is strongly controlled by surface (stomatal) conductance, i.e by physiological limitations to transpiration by the vascular vegetation (Admiral et al. 1997, Kellner 2001). By contrast, ET is more strongly controlled by the amount of solar radiation in moss-dominated peatlands (Kurbatova et al. 2002). Moss surface conductance to water vapor transfer has also been found to vary with moss water content (Williams and Flanagan 1996). In addition, the plant canopy and litter above the moss layer restricts energy exchange and turbulent transfer of water vapor between the moist peat and the air above, further inhibiting evaporation in many peatlands (Campbell and Williamson 1997).

Hydrology and peatbog development

Ombrotrophic peatlands are not common in central Europe. Continental and subcontinental climates with prolonged warm and dry summers are not suitable for widespread peat formation and bog development. This holds also for the Třeboň Basin with rather low precipitation (annual average 650 mm) and high mean temperatures (annual average 8°C).

There are several models that described the origin of bogs in a dry climate. The initial development of bogs has been linked to the headward erosion of streams, which create local watershed divides. This mechanism was proposed by Kulczyńsky (1949) for the formation of bogs in the Polesie and was later applied to the Myrtle Lake peatland of Minnesota (Heinselman 1970). According to this hypothesis, precipitation leaches inorganic solutes from the surface waters of the interfluves, facilitating the invasion of *Sphagnum* and formation of a raised bog.

Development and hydrology of peatlands was broadly studied by Glaser et al. (1997) in relatively arid region of north-western Minnesota. Discharge zones may represent an essential precursor for bogs in this area. Water table mounds will form in discharge zones, producing a thinner aerobic layer and more rapid peat accumulation. Despite the close linkage to groundwater the bog vegetation remains isolated from minerotrophic water by converging system in moist periods and by substantial draw-down of the water table during droughts.

Aims of the thesis

A massive dieback of *Pinus rotundata* was observed in many peatbogs in the Třeboň Basin in the mid-1980´s (Liška et al. 1989, Ferda 1991, Rektoris 1994, Rektoris et al. 1997). Long-term changes of water régime are considered to be the most probable reason for this situation. Additionally, the decline of *P. rotundata* has been recorded area-wide in other disturbed bogs during the last 30 years, e.g., in Schwarzwald (von Sengbusch et Bogenrieder 2001), Schweizer Jura (Freléchoux et al. 2003) and south-western Poland (Boratyński 1994). This area-wide dieback has stimulated several studies of different aspects of *Pinus rotundata* ecology (e.g., Schmid et al. 1995, Rektoris et al. 1997, Businský 1998, von Sengbusch et Bogenrieder 2001, von Sengbusch 2004, Mach 2007, Bastl 2008) including this thesis.

At the early beginning of my thesis, the only information about the hydrology of the *Pinus rotundata*-dominated peatbogs was already published by Neuhäusl (1975). These data were based on the field work made in the Velké Dářko peatbog at the beginning of the 1950´s. Therefore the general aim of my thesis was to fill this information gap by studying various aspects of the water régime of *Pinus rotundata*-dominated peatbogs in the Třeboň Basin (i.e., transpiration, water table fluctuation, successional changes, water retention capacity), starting at the species level towards the whole peatbog level.

Experiments in controlled environments are now the most common scientific method used in ecological studies. Therefore we can find a great number of studies devoted to the ecology of tree seedlings which represent an ideal object of the experimental approach. Even if seedlings are crucial for the next survival of a given species, we should not ignore mature trees which create the "forest environment" and produce seeds. Available information about the ecology of many endemic tree species is still scarce and further research is needed.

The thesis consists of four original studies:

I. Kučerová A., Čermák J., Nadezhdina N. & Pokorný J. (2010): Transpiration of *Pinus rotundata* on a wooded peat bog in central Europe. – Trees 24(5): 919-930.

II. Kučerová A., Rektoris L., Štechová T. & Bastl M. (2008): Disturbances on a wooded raised bog – How windthrow, bark beetle and fire affect vegetation and soil water quality? – Folia Geobotanica 43: 49-67.

III. Kučerová A., Rektoris L. & Přibáň K. (2000): Vegetation changes of *Pinus rotundata* peatbog in Žofinka Nature Reserve, Třeboň Biosphere Reserve. Příroda 17: 119-136, Praha.

IV. Kolmanová A., Rektoris L. & Přibáň K. (1999): Retention ability of Bog Pine peat bog ecosystem and its response to downpour precipitation. – In: Vymazal J. [ed.], Nutrient Cycling and Retention Ability in Natural and Constructed Wetlands., 177-182 p., Backhuys Publ., Leiden.

More specifially, in the studies presented I asked following questions:

1. How high is the transpiration of *Pinus rotundata*? Is it reasonable to expect unlimited transpiration thanks to high soil water saturation? Can the transpiration sums and precipitation be used as a proxy for the water table fluctuation?
2. Has a tree layer break-up any effect on the water régime of a peatbog? What is the perspective of the endemic *Pinus rotundata* in a windthrow–bark beetle affected sites?
3. What was the post-fire colonization in a *P. rotundata*-dominated peatbog? Are there any differences in vegetation and soil water quality at three differently disturbed sites: a burned site, a windthrow–bark beetle affected site, and an undisturbed *P. rotundata* bog forest?
4. What are the basic rules of the water retention capacity in *P. rotundata* dominated peatbogs? Can these peatbogs function as a big sponge catching and absorbing most of the rainfall?

MATERIAL AND METHODS

Study sites

The Červené blato bog (48°52´ N, 14º48´ E, 465–475 m a.s.l.) is located in the southern part of the Třeboň Basin Biosphere Reserve (Fig. 3). It is a continental raised bog (sensu Neuhäusl 1972) or forested/wooded peatbog with the largest population of *Pinus rotundata* and its hybrids with Scots pine (*Pinus* × *digenea* G. Beck). The bog surface is very sligthly domed. Maximum peat depth is about 7.6 m (Weis 1965). A detailed description of the vegetation dynamics on the locality was given by Rektoris (1994) and Jeník et al. (2002). The *Vaccinio uliginosi-Pinetum rotundatae* (Oberdorfer, 1934) community represents the most common vegetation type on the locality. *Pinus rotundata* is the main woody species, also *Picea abies* and *Pinus sylvestris* occurred there. The bog forests were usually more than a hundred years old, often dense and tall and are similar to the northern taiga ecosystem (Jeník et al. 2002). The shrub layer included many young *P. rotundata* trees, less abundant were *Frangula alnus* and *Betula pendula*. The herb layer consisted mainly of ericoid species (*Vaccinium myrtillus, V. uliginosum, Ledum palustre*) and graminoids or cyperoids (*Molinia caerulea, Eriophorum vaginatum*). The moss layer consisted of several *Sphagnum* species, *Dicranum* and *Polytrichum* spp. A part of the bog was disturbed by peat digging in 19th century. After termination of peat digging the pits were flooded. More recently, *Sphagnum fallax, S. flexuosum* and *Eriophorum vaginatum* dominated in those stands (close to the ass. *Eriophoro vaginati-Sphagnetum recurvi* Hueck 1925).

Jankovská (1978, 1980) described the development of the locality during the Holocene. The vegetation had minerotrophic character until the young Atlantic period. During the young Atlanticum the first pines occurred and the first communities of the alliance *Pino-Ledion* were established. Bog pine woodlands were several times destroyed by fire during both older and younger Subatlanticum, but they repeatedly regenerated.

Spitzer et Jaroš (1993) found very important relic species (tyrphobionts) of Lepidoptera in the open wet forests or in successional stages after peat digging (open *Sphagnum* carpet). On the contrary, the relic fauna of closed bog pine forest was much less diverse and composed mostly of abundant tyrphophilous and tyrphoneutral forest species. The presence and survival of both tyrphobiontic and tyrphophilous relic insect species seem to provide good evidence of the long-term presence of open peatland habitats during the Holocene at this locality (Spitzer et al. 1991).

The Žofinka peatbog (130 ha, 48°49´N, 14°53´E, 470–475 m a.s.l) is located 22 km south of Třeboň (Fig. 3).Valuable *Pinus rotundata* stands have also been found at this study site until windbreaks in the late 1970´. Both the past and recent vegetation was described in detail in Study III.

The peatbog is situated in a shallow depression of the Cretaceous bedrock. The bedrock is made up of sediments of the Klikov series – sand, clay and clayish sand (Koroš et al. 1998). The bedrock is very acid and poor in nutrients. According to Koroš et al. (1998) the peatbog originated from a gradual local subsidence of the Cretaceous bedrock, consequently followed by a local increase of water table. The bog surface is flat. Maximum peat depth is about 4 m. A part of the peatbog was affected by peat digging in the 1950´s, the surface layer was cut off by about 1 m (Kučera 1977).

Methods

Methods used are broadly explained in particular studies. In the following paragraphs only short summary is given and some methods are discussed in terms of their relative advantages and disadvantages for the bog pine-dominated peatbogs under the study.

Components of the water balance

Long-term monitoring of water table fluctuation, discharge, precipitation and microclimate was the main source of data for the evaluation of water balance of *Pinus rotundata*-dominated peatbogs. In both study sites altogether 56 pipes were installed (1.5 m long, perforated PVC pipes, diameter 5,0 cm) for the groundwater table (WT) monitoring. WT was measured regularly weekly during 1995-2000 with the accuracy of ± 5 mm. The outflow was measured in three main drainage channels by the Thompson overfall. In each study site three small ombrometers were installed in 1995 (Hellmann type, diameter 159,8 mm) and weekly sums of precipitation were recorded. During the winter (IX-III) precipitation data were acquired from the nearest meteorological station in Byňov, Nové Hrady (cca 4 km appart). Daily mean air temperatures (accuracy of ± 0,5°C) and relative air humidity (accuracy of ±2%) were measured using three thermohydrographs (Novi, Czech Republic) installed in standart meteorological screens (at a height of 2 m, two in Červené blato, one in Žofinka peatbog). Data were logged as hourly values.

Additionally the experimental plot (in Červené blato peatbog, Study I) was equiped by an automated datalogger (MS16, Fiedler-Magr, Czech Republic) connected to the thermistor thermometer (accuracy of ± 0,1°C) at a standard meteorological screen, to an automated raingauge (SR02, installed in a treeless gap in the forest close to the experimental plot) and to a single submersible pressure transducer for measurement of depth to the water table in high temporal resolution (every 15 min, LMP307 sensor, Fiedler-Magr, Czech Republic).

Spatial variation of the water table within the experimental plot was estimated manually once a week in a regular network (grid spacing 10 m) of 16 dipwells (1.5 m long PVC pipe, 5 cm diameter). Soil moisture content was measured using VIRRIB sensors (Amet, Czech Republic) at three different depths (15, 25, and 35 cm) and estimated manually once a week.

In addition, both air temperature and global radiation were measured at a meteorological station in the Institute of Botany at Třeboň, 20 km north of the experimental site. Here, global radiation was measured at intervals of 10 min using a Kipp Zonen radiation sensor mounted on a 10 m high mast, and air temperature with a thermistor thermometer in a standard meteorological screen. There were only minor differences in climatic conditions between the experimental site at the Červené blato peatbog and the meteorological station at Třeboň. The data were used especially for the calculation of the potential evapotranspiration in the Study I. Daily potential evaporation (PET, expressed in mm day^{-1}) was calculated using the simple equation of Türc (1961), which was positively evaluated by Federer et al. (1996).

Estimation of (evapo)transpiration

Various methods have been used to quantify the evapotranspiration rate in mire ecosystems, including the energy-balance method (Přibáň and Ondok 1985, 1986, Roulet and Woo 1986, Lafleur 1990, Lafleur et Roulet 1992), the eddy-correlation method (Linacre et al. 1970, Kelliher et al. 1998), the water balance method (Baden and Eggelsmann 1964), the diurnal fluctuation water-table method (Heikurainen 1963, Dolan et al. 1984, Laine 1984), and different lysimetric techniques (Eggelsmann 1964, Chapman 1965, Bay 1966, Bernatowicz et al. 1976, Koerselman et Beltman 1988). Different models and micrometeorological methods used to estimate wetland evapotranspiration were recently broadly reviewed by Drexler et al. (2004).

The selection of an appropriate method is especially complicated in the case of wooded peatbogs because most methods can be used only with a special equipment adapted to the forests (special tall tower, very accurate sensors, etc.). Such equipment is usually very expensive and can be hardly constructed on quite unstable peaty soils. Therefore, despite a vast amount of literature on evapotranspiration from treeles peatlands, there is still a very limited number of studies devoted to the evapotranspiration or transpiration of wooded peatbogs (e.g., Belotserkovskaja 1975, Neuhäusl 1975, Kelliher et al. 1998, Admiral et Lafleur 2007).

For the estimation of transpiration of *Pinus rotundata* forest we used the measurement of sap-flow inside six experimental trees. The sap flow method provides a direct estimate of the upward water movement inside individual trees in the stand. Transpiration measured by sap flow method showed good agreement with total evaporation measured by the eddy-correlation method (Lundblad et al. 2001, Meiresonne et al. 2003). There are several systems for measuring sap flow velocities, e.g., the heat-dissipation method (Granier), tissue heat-balance method (Čermák) or heat field deformation method (Nadezhdina). Without compensation, natural temperature gradients may cause large errors in measurements made by the Granier system (e.g., Lundblad et al. 2001). Therefore radial flow patterns must be considered when calculating total tree sapflow (Hatton et al. 1995, Čermák and Nadezhdina 1998, Lundblad et al. 2001). Heat field deformation method (Nadezhdina et al. 1998) used in our study combinated with the radial pattern of sap flow offers a suitable tool for estimating the transpiration of individual trees and also the possibility to scale-up to the whole stand level. However, many assumptions are required in the up-scaling approach. The stand transpiration estimates depend on a sub-sample of trees that is assumed representative of the population of trees within the stand. In addition, up-scaling from the sample trees to the whole stand requires an accurate estimate of the distribution of suitable biometric parameters of the stand (Čermák and Kučera 1990) - in this study we used non-linear regression between the daily tree sap flow and the tree basal area.

Soil water chemistry

In the Study IV seasonal monitoring of soil water quality was used to specify the effect of vegetation changes on peatbogs chemistry. We have chosen the monitoring of soil water instead of analysing the chemistry of peat soil samples because most nutrients are bound into the organic complexes in a peat soil and some nutrients may not be available for plants at all. Additionally, different soil extraction procedures give different results and their intercomparison with other studies is rather difficult. Therefore, we suppossed the soil water samples may be better predictor of the nutrient availability for plants. However, the soil water quality is highly variable during the year (as a result of precipitation water quality, rate of mineralisation or rate of plant nutrient uptake), therefore it was necessary to take up soil water samples several times during the year (Navrátilová et Navrátil 2005).

RESULTS AND DISCUSSION

Most of the more specific conclusions of the study emerge from the individual papers. This chapter is therefore devoted to a brief concluding discussion of some general topics. I will also focus on my unpublished data and their relation to the main contents of this PhD. study. The papers will be referred to by Roman numerals, e. g., [I, IV].

Water balance of the *Pinus rotundata* bog forest, Třeboň Basin

In this chapter, I will focus on a detailed description of particular water fluxes at our experimental plot (Červené blato peatbog) which represents a typical mature bog pine forest in the Třeboň Basin. Additionaly, the soil water budget is calculated for this forest stand.

The most important water fluxes were measured: precipitation, discharge [IV], tree transpiration [I], water table fluctuations and changes of soil water storage (Fig. 4).

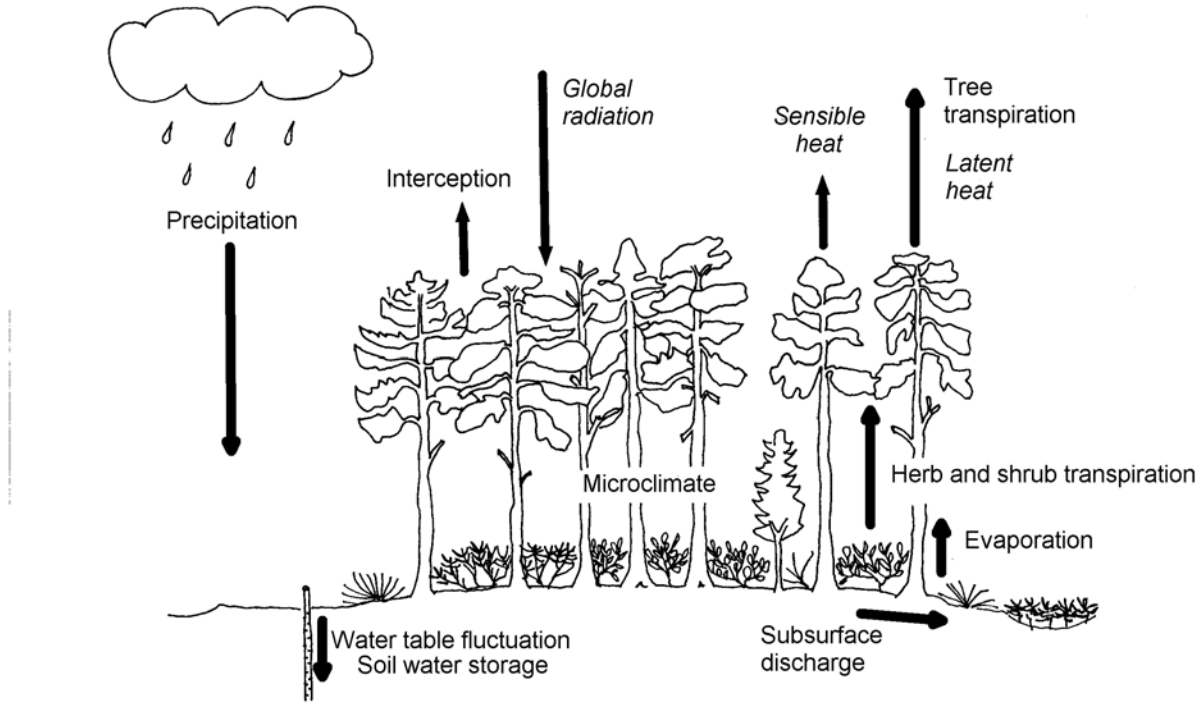

Fig. 4.: The most important water fluxes at the experimental plot studied (as. *Vaccinio uliginosi-Pinetum rotundatae*). The most important energy fluxes are illustrated in italics.

Precipitation was the main recharge term, the most important was the sum of vertical precipitation during the vegetation period. The mean (1995–2000) for the Červené blato peatbog was 450 mm from May to October, and 700 mm for the whole year (unpubl. data). Horizontal precipitation was probably unimportant for the whole water balance (probably max. 10 %), but it has not been measured at all in the Třeboň Basin. Nevertheless, several species of the herb and moss layer could profit from the regular occurrence of heavy dew in summer and of almost regular fog in autumn. A part of both vertical and horizontal precipitation is intercepted on the soil and vegetation surfaces, but this interception was not measured during our study. We may supposse that the interception could be within the range

of 25–35 % according to the study conducted by Neuhäusl (1975) in the Velké Dářko peatbog. Non-intercepted precipitation infiltrated into the soil and reached the water table very quickly, within several minutes [IV].

Surface recharge is common only in the peripheral parts of the peatbog, which is manifested by the occurrence of a different vegetation – by the waterlogged spruce forests.

Recharge from the mineral bedrock towards the water table is probably minimal because deep peat layers (down to 6 m in our experimental plot, unpubl. data) had a very low hydraulic conductivity. Additionaly, the bedrock in most of the area consists of clay or clayish sand, also with a low hydraulic conductivity. We supposed that only the deepest peat soil layers could be locally saturated with water from mineral bedrock (Rektoris et al. 1997). However, the costly direct measurements (pumping tests) have not been conducted yet.

Discharge of water (both surface and subsurface) depends on: (i) the slope, (ii) the distance and location of a given site from the drainage network, and (iii) on the actual depth to the water table [IV]. Surface discharge is significant along drainage channels and in the formerly extracted parts of the peatbog, especially in winter, early spring and after heavy rains [IV]. Surface discharge from the whole peatbog (from one catchment drained by a single drainage channel) was calculated in [IV]. Typically, the surface discharge reached high rates immediatelly after heavy rain and during high water table episodes. On the other hand, there were long periods with almost zero discharge in summer [IV].

Inside our experimental plot, the surface discharge was not detected. The subsurface discharge was probably fully compensated by subsurface recharge, and both processes were limited to the highest water table episodes (unpubl. data).

Evapotranspiration includes three main components: (i) tree transpiration, (ii) transpiration of the shrub and herb layer, and (iii) evaporation from the soil and vegetation surfaces.

(i) Tree transpiration was the main topic of [I]. The maximum and mean daily canopy transpiration rates were 3.0 and 1.8 mm per day, respectively, and were thus similar to or little higher than other published rates for Scots pine (cf. Meiresonne et al. 2003, Vincke and Thiry 2008). Interestingly, there was an upper limit to transpiration in the investigated trees of *Pinus rotundata* even when the soil water supply was not limiting. We reported limited sap flow rates especially under conditions of high vapour pressure deficits (VPD) in summer [I]. Similarly, Saugier et al. (1997) reported low transpiration rates in a *Pinus banksiana* boreal forest even when the soil was well supplied with water. They attributed them to a marked reduction of stomatal conductance as vapour presssure deficits increased. Additionally, Humphreys et al. (2006) reported a decline in surface conductance with increasing VPD indicating physiological restrictions of transpiration, particularly in peatlands with woody vegetation. Water transport efficiency is likely to limit the rate of transpiration in trees, especially in conifers with narrow tracheids. However, the stomata can close in direct response to increasing VPD without any decline of plant water potential (Lambers et al. 1998). Water loss is therefore restricted when dry air is likely to imposse water stress (Schulze 1986) and transpiration can be almost constant over a range of high VPDs. The limited transpiration of *Pinus rotundata* under conditions of high VPD (or advection of dry air) can be advantageous in maintaining a suitable water balance of a peatbog. In contrast, several wetland broad-leaved trees and shrubs such as *Alnus glutinosa*, *Frangula alnus*, *Betula* sp. and *Salix* sp. can transpire at high rates even when the VPD is high (Čermák et al. 1984; Přibáň and Ondok 1986). Thus, long-term changes in tree composition leading towards the domination of a peatbog by these broadleaved trees/shrubs could accelerate the water table drawdown and cause further vegetation changes, [III].

The total seasonal transpiration (25 April–20 October 2000, 180 days) amounted to 322 mm, or 62 % of the potential evapotranspiration over this period. This canopy transpiration

was compensated by 319 mm of precipitation. Similar values of seasonal stand transpiration were estimated, e. g., by Cienciala et al. (1994) for spruce forests in SE Sweden (mean daily transpiration 1.6 mm, seasonal total 325 mm over 190 days, ratio of seasonal stand transpiration to potential evapotranspiration 68 %). Therefore the canopy transpiration values we obtained for *Pinus rotundata* were similar to those recorded for many coniferous forests in Europe (Köstner 2001, Roberts 2007).

(ii) Unfortunately, the transpiration of the shrub and herb layer has not been quantitatively measured. Grelle et al. (1997) estimated the understorey contribution at 15 % of total evapotranspiration for a 50-year-old boreal forest in Sweden, and a similar understorey evapotranspiration was estimated by Vincke and Thiry (2008) for a Scots pine forest on sandy soil (18–20 % of the stand water use). Generally the transpiration rates of ericoid shrubs (dominants of the ground layer in our experimental plot) can be lower (compared to mesophytic herbs). Their stomatal conductance is usually also reduced as vapour pressure deficits of the air increased (Admiral et Lafleur 2007, Kolmanová 1997, Woodward 1986). Nevertheless, *Vaccinium myrtillus* was the dominant understorey species in our experimental plot. This deciduous ericoid shrub has probably a very low transpiration rates during April because leaf expansion is not complete until the middle of May. Then the herb layer transpiration represented an important flux from the middle of May to the middle of September (leaf senescence).

(iii) Evaporation from the soil and soil vegetation (= moss layer) is probably highly variable due to their variable moisture content. It could account for 10 % of the total stand evaporation with rates of 0.1-0.6 mm per day inside a boreal spruce-pine forest according to Constantin et al. (1999). In our experimental plot, the soil was almost completely covered by the moss layer, which hampered soil evaporation. Evaporation from the moss layer may be limited to times of maximum water saturation in early April and/or after rains. For example, Heijmans et al. (2004) reported the evaporation from a moss carpet in a boreal forest as low as 0.3 $mm.d^{-1}$. Moreover, Neuhäusl (1975) reported almost zero evaporation from the soil and moss layer during a dry period in summer. We can similarly assume the moss layer evaporation to be 0.3 $mm.d^{-1}$, but only during wet periods after a rain (precipitation higher than cca 2 mm, which can already reach the moss surface); then the evaporation probably ceases due to the moss dryness (water table is always too low to saturate mosses by capillary flow, Neuhäusl 1975).

Changes of soil water storage and/or water table fluctuations were partly described in [III] and [I]. The seasonal fluctuations of water table can be described as follows: In winter, after the bog freezes, precipitation (esp. snow) accumulates on the surface rather than recharging the bog, causing the water table stagnate or even slowly decrease. When precipitation comes in the form of rain (sometimes during short episodes of warm weather in winter), and the bog remains frozen, the rain water does not accumulate, and most of it outflowed the bog surface. In a very mild winter, the highest water table will occur. If the frost period continues over the whole winter, melting snow saturates the peat profile during early spring. In summer, soil water storage (as measured by water table fluctuations) was found to be very sensitive to both ET and precipitation (Heikurainen 1963).

Treeless gaps showed smaller water table fluctuations = smaller changes of soil water storage (mean water table depth 18.6 cm below ground) than the undisturbed *Pinus rotundata* forest (mean water table depth 25.5 cm below ground), especially during the vegetation period. By contrast, during winter and early spring, the differences between both sites become negligible. This demonstrates a great impact of the tree transpiration on the water balance of a *Pinus rotundata* dominated peatbog [III].

Soil water budget

Pronounced changes in the water table depth clearly followed the calculated differences (in mm) between the accumulated precipitation and accumulated transpiration (D = P – T) [I]. Therefore we tried to apply a simple soil water balance equation (Benetin et al. 1969) which can be used for the derivation of the **daily values** of evapotranspiration. We also compared these values with the measured data of tree transpiration and/or with the calculated potential evapotranspiration sums. However, we **failed** with this approach. The reason could be that the simple soil water balance equation is not suitable for soils with a very shallow water table (Benetin et al. 1969). There is an important flux from a shallow water table towards the unsatured zone (capillary fringe). This water can be immediately used by plants for their transpiration. However, this flux could not be included into our calculation with available data at the given time-scale. Such simple water balance calculations are quite reliable for longer time periods like a week, month or vegetation period.

Instead, a simple long-term water budget was done for the experimental plot in [I]. A suitable period for such a calculation was identified as 01 April–07 August 2000. For this period, the value obtained from the soil water budget was 247.6 mm (i.e., 1.9 $mm.day^{-1}$) and from the scaled-up sap flow data 257.8 mm (i.e., 2.0 $mm.day^{-1}$). This means that tree transpiration (derived by scaling up the sap flow measurements to the stand level) accounts for almost 100 % of the whole-stand evapotranspiration and that the (evapo)transpiration of both the herb and the moss layer may be almost negligible. This contrasts with the findings of Grelle et al. (1997) and Vincke and Thiry (2008) (herb and moss layer evapotranspiration cca 15–20 % of the stand water use). This discrepancy may be partly attributable to the uptake by vegetation of water from the unsaturated layer above the water table, which was not included in this soil water budget calculations. Additionally, the peat matrix usually exhibits a hysteresis effect during wetting and drying cycles – the rise in water table "consumed" more water than its drawdown (Weiss et al. 2006). This effect can be seen in [I] - Fig. 6, where the measured water table more closely mimicked the difference between accumulated precipitation and transpiration during drying (first half of the vegetation period) than during the wetting period after heavy rains in early August. Unfortunately, we have no data to assess the impact of the hysteresis effect on our soil water budget.

It can be concluded that the *Pinus rotundata* peatbogs in the Třeboň Basin exist within a summer moisture-deficit regime whereby the evapotranspiration is the dominant water flux. As such, these peatbogs are extremely susceptible to both climatic variability and human impact that may upset the tense balance between water inflow = precipitation and water outflow = evapotranspiration.

Ombrotrophic peatbogs in the Třeboň Basin

According to basic meteorological characteristics (mean annual temperature, precipitation, potential evapotranspiration, Přibáň et al. 1992, Šebek 1978) the Třeboň Basin is relatively climatically dry region, especially when compared with the mountain areas where most ombrotrophic bogs are located in Central Europe (e.g., Šumava Mts.). Therefore the presence of ombrotrophic bogs in the Třeboň Basin requires some special mechanisms to mantain positive water balance.

Pinus rotundata dominated peatbogs in the southern Czech Republic (so called „blata") were classified as classical raised bogs by several authors (i.e., as peatbogs saturated only with water from precipitation, e.g., Rudolph 1917). On the other hand, some authors (Spirhanzl

1951, Holubičková 1960) pointed out higher concentrations of Ca in their soil and water in comparison with the mountain raised bogs. Therefore they denoted them as transitional peatbogs, i.e., peatbogs in which the vegetation is partly saturated by water from the mineral bedrock. *P. rotundata* dominated peatbogs also have several specific features: (i) they are usually located in a valley (e.g., along the Vltava river in the Šumava Mts.); (ii) they have an only slightly domed peat surface in contrary to the classical domed raised bogs. Nevertheless like the typical raised bogs, they have a low pH and low cation concentrations, similar vegetation and similar peat composition (Válek 1947).

There are no doubts that the initial accumulation of organic matter in peatbogs in the Třeboň Basin has been possible only in terrain depressions under the influence of water from the mineral bedrock (Procházková 1978). Therefore the basal peat layers consist of remnants of *Carex* sp. and/or *Phragmites*. Remnants of *Sphagnum* and other oligotrophic species have occurred since the Atlantic period (Jankovská 1978) when the influence of water from the mineral bedrock on the surface vegetation declined due to the thickness of accumulated peat.

The basic water balance of the *P. rotundata* dominated peatbog was described in the foregoing chapter. From above follows, that the surface vegetation was saturated only with precipitation water, like in typical raised bogs. Water from the mineral bedrock may influence only the marginal parts of the peatbogs and/or probably saturates the deepest peat layers. This hypothesis is in agreement with the finding of Rektoris et al. (1997).

Slightly higher concentrations of Ca and other cations in both soil water [II] and peat soil in comparison with mountain peatbogs (cf. Rybníček 2000) can be interpreted as an undirect effect of the lower total precipitation, and consequently of lower water outflow. This smaller total outflow of water with dissolved cations results in their higher concentrations in soil water in the Třeboň Basin peatbogs. Additionaly, lower precipitation along with higher retention are probably the main reasons for high concentrations of dissolved organic carbon (Hruška 1999) and very high concentrations of protons in the soil water (i.e., high acidity, pH = 3.4, [II]) in the Třeboň Basin peatbogs. High acidity can positively affect the long-term stability of the bog vegetation – there is only a limited set of species that can survive in such harsh environment (Ellenberg 1996). On the other hand, such high acidity may represent a serious threat for the long-term survival of *Pinus rotundata* (von Sengbusch 2004).

"Compensation peat growth"

The key predisposition for the formation of large ombrotrophic peatbogs in the Třeboň region is probably the long-term slow subsidence of its tertiary bedrock (Koroš et al. 1998, Procházková 1978). The subsidence is not regular throughout the Třeboň Basin and it is more intense in locations of tectonic disturbances (Vyskočil 1994), i.e., along its north-south axis and at its eastern margin where most of the *Pinus rotundata* dominated peatbogs occur. Under suitable condition (wet climate) this slow subsidence (approx. 1-2 mm per year, Vyskočil 1994) should be compensated with accumulation of peat in a water-saturated environment (estimated at 1.8-2.0 mm per year by Vymazal et al. 2011). Therefore these peatbogs are not growing upwards forming the domed peatbog surface; instead, they "grow down" compensating the very slow bedrock subsidence by slow peat accumulation. The only slightly domed surface means the low discharge, i.e., improvement of their water balance in comparison with the more domed peatbogs where discharge represents a more important water flux.

A different case can be the famous Borkovická blata peatbogs which are connected with very special geological conditions. There is an abrupt disruption in the bedrock, which initiated the discharge of artesian water towards the surface. In this case, the development model described by Glaser et al. (1997) and already mentioned in the Introduction should explain the existence of ombrotrophic *Pinus rotundata* peatbogs within this peatland complex.

Moreover, the contrasting phenology between vascular plants and mosses can play an important role in the survival of the moisture demanding sphagna in these relatively climatically dry peatbogs. In summer, sphagna can benefite from the moderate shading of sparse tree canopy during high irradiance period as reported by Hájek et al. (2009) or the mosses are rather inactive (due to low water content) during several weeks in summer. However the mosses can be fully active during early spring and in later autumn, profiting from the absence of a long-lying snow cover, full water saturation and non-stress temperatures.

Is *Pinus rotundata* dieback associated with the long-term changes following drainage?

According to several authors (Neuhäusl 1972, Spitzer et Jenik 2002) the bog pine forests represent islands of the northern taiga within central Europe. Abrupt vegetation changes or catastrophic disasterrs (heavy windstorms, insect infestation and fire) are, in fact, disturbances characteristic of such coniferous forests (Frelich et Reich 1995, Jonášová et Prach 2004).

The formation of a closed bog pine forest was induced by artificial drainage at the beginning of 19th century, as follows from the literature survey. Domin (1904) reported maximally 6 m tall bog pine trees from the Červené blato peatbog in 1902. An unpublished peat sampling survey (Kučerová et al. unpubl.) found a little or moderately decomposed sphagnum peat starting from 20-30 cm below the soil surface. The former open peatbog with only scattered bog pine trees and a vigorous wet *Sphagnum* carpet offered favourable conditions for massive *Pinus rotundata* seedling establishment induced by moderate drainage at the beginning of the 19th century followed by the development of a closed bog pine canopy (Schmid et al. 1995, von Sengbusch 2004, Cedro and Lamentowicz 2008).

An increase of tree-growth potential (increase in both tree height and radial increment) in peatbogs after drainage has been reported by several authors (e.g., Schmid et al. 1995, Freléchoux et al. 2000b etc.); several authors (e.g. Laine et al. 1995, Laiho et al. 2003) supposse it to be a general trend in the vegetation succession in mires affected by water-level drawdown. Additionally, the abundance of trees also increased, which greatly increased the shading of the moss layer.

So, why large-scale *Pinus rotundata* dieback has been documented since the 1980ies on sites where vigorous forests were originally found until this time? The answer is not simple. There are several possible explanations.

Acidification

We suppose strong water acidification since the construction of drainage systems in the bog pine dominated peatbogs in the Třeboň Basin. Unfortunately, we have only indirect evidence of it: (i) Drawdown of the water table is invitably connected with peat mineralisation and acidification (Laine et al. 1995, Laiho et al. 2003, Mitsch and Gosselink 2007), (ii) these peatbogs have the most acidic soil water (pH 3.4) of all peatbogs in the Czech Republic, sampled in the complex study made by Hruška (1999), and (iii) Vilhelm (1900) and Domin (1904) documented the occurrence of several nutrient-demanding species (*Utricularia neglecta, Naumburgia thyrsiflora, Cicuta virosa*) in the drainage channels in the Červené blato peatbog. This means that the surface water was probably less acidic and richer in nutrients 100 years ago.

The present high acidity [II] is connected with very low concentrations of available cations (Ca, Mg), which is suppossed to be the main reason for the dieback of *Pinus rotundata* in southern Schwarzwald (von Sengbusch 2001, 2004).

Windbreaks – disproportion between tree height and limited root system

Moderate drainage increased the growth potential of trees - both tree height and radial increment changed rapidly. However, the trees also increased their height:diameter ratio, as reported by von Sengbusch (2004). The successive disproportions between the height of the trees (up to 18 m) and a still shallow root system (often limited to 20–40 cm below ground owing to a high water table in some periods of year and/or toxic conditions in deeper peat layers) can have diminished the stability of the trees in the unstable peaty soils, thus increasing the probability of windbreaks. Therefore windbreaks, both on a small-scale and large-scale, have been quite common in *Pinus rotundata* dominated peatbogs since the 1970ies [II, III, Rektoris et al. 1997, Rektoris et al. 2003], followed by other disturbances typical of coniferous forests, such as insect infestation or fire [II, III].

Sinking of mature trees

We frequently found dead full-grown/mature trees in some parts of the peatbog, where relativelly porous peaty soil occurs. Such trees probably died due to succesive sinking of their root systems into the soil, after having reached the weight which the soil was unable to sustain. In deeper peat layers, the sunken roots suffered from lack of oxygen and the trees started to die.

Failure of drainage systems – mature trees have only limited adaptability to new hydrological conditions

Peat extraction closely connected with intensive drainage was mostly abandoned at the beginning of 20th century in the Třeboň Basin; it continued only in some localities until the 1950ies (Borkovice). Since that time, the drainage network has not been maintained more. The drainage channels started to lose their function and the water table steadily increased in their immediate surroundings. But mature trees growing along the drainage channels are usually unable to change the position of their roots originally adapted to a lower water table. Such trees started to suffer from lack of oxygen because the increased water table flooded their roots and they even started to die. Such a situation is nowadays quite common along drainage channels in the Červené blato peatbog, especially after the blocking of the main drainage channel in 1990ies.

Limited seedling recruitment

Low seedling recruitment is the next seriuos problem for the long-term survival of *Pinus rotundata* (Bastl 2008, von Sengbusch 2004). *P. rotundata* can germinate well in a moderately wet *Sphagnum* carpet under favourable light conditions, i.e., on open peatbogs sites with a low cover of ericoid shrubs (*Vaccinium myrtillus, V. uliginosum*) and only scattered trees. However, bog pine seedlings are almost absent in stands with a high cover of *V. myrtillus* due to the absence of an open sphagnum carpet and limited light. Unfortunately, nowadays most formerly drained stands of *P. rotundata* have a dense cover of *V. myrtillu*s and only a loose cover of sphagna. In these stands, the seedlings of *P. rotundata* are found only occasionally in the wet area of windthrows. The absence of seedlings and young trees is the most serious problem especially in southern Schwarzwald (Schmid et Bogenrieder 1998, von Sengbusch 2004) as well as in the Borkovická blata Nature Reserve in the northern part of the Třeboň Basin (Abazid et Kučerová, unpubl. data).

Heavy snowfall

Young stands of *Pinus rotundata* are occasionally threatened by heavy snowfall. The trunks of young trees are bent during the epizodes of high cover of wet and heavy snow. Large scale disruptions of the stands were sometimes documented, e.g., in January 2007. High incidence of snowbreaks is probably due to a high vertical growth rate of trunks under the conditions of high competition for light with neighbouring trees.

Dieback as an artefact of the climax forest hypothesis – autogennic succession?

There is also, one say, heretical hypothesis which could partly explain the almost synchronous decline of bog pine dominated forests in this country. A forest stand is usually designated as a nature reserve at its optimal stage of development, i.e., at its climax stage when most of the dominant tree species have reached the maturity. A few decennary later, this stand naturally reaches the final stage of tree life – tree senescence. As most forest nature reserves were established during the 1950-1960ies at the mature stage of their development (which is usually the most favoured one by nature conservation authorities as a so-called climax forest), we can witness the natural decline of such forest stands now, i.e., some 40-50 years later. Therefore the decline of these forests can also be considered as a part of their natural autogennic succession (Neuhäusl 1992).

Additionally, it is of interest that the decline of *P. rotundata* is a seriuos problem in the Czech Republic, while the expansion of the same species is, in some cases, a problem in Switzerland (Freléchoux et al. 2000b). If we suppose that trees in both countries belong to the same species (which is not sure, see Introduction), this fact implies that in Switzerland the authors have documented the formation of new bog pine forests as a result of drainage – the same process that took place in the Czech Republic in 19th century.

Available evidence indicated that the long-term changes following drainage (i.e., complex changes of tree growth form, both tree and ground layer species composition, changes in soil moisture saturation and soil water quality in terms of 100-200 years) may be the main trigger for the large-scale decline of *Pinus rotundata*. In addition the decline of these forests can be considered as a part of their natural autogennic succession (Neuhäusl 1992).

Future of *Pinus rotundata* in the peatbogs of the Třeboň Basin

Pinus rotundata represents one of the stress-tolerant species which can sustain a high water table ([I], Bastl 2008), high acidity and lack of nutrients (von Sengbusch 2004). All these environmental conditions are typical of ombrotrophic peatbogs. Therefore *P. rotundata* could survive several thousands of years in peatbogs (Jankovská 1980). Even if the growth of *P. rotundata* was enhanced after drainage (e.g., Freléchoux et al. 2000a, Freléchoux et al. 2000b, von Sengbusch 2004), the drainage is invietably followed by the expansion of other more competitive species (*Pinus sylvestris, Picea abies, Betula pendula*). Additionaly, after drainage, the cover of ericoid shrubs increased followed by the retreat of a vigorous *Sphagnum* carpet (Domin 1904). The subsequent increase of abundance of *Vaccinium myrtillus* limits the *P. rotundata* seedling recruiment and growth (Schmid et al. 1995, Bastl et al. 2009, [III]). Thus, a high groundwater table plays a crucial role in the long-term stability of natural *P. rotundata* populations (Rektoris et al. 1997). ”No action” management plan for *P. rotundata*-dominated peatbogs is not a suitable tool for preservation of the species in those peatbogs where the water regime has been altered by drainage. Successive and cautious raising of the groundwater table, by blocking the drainage ditches, may partly suppress the

establishment of *P. abies* and *P. sylvestris* and will support the seedling recruitment of *P. rotundata* (Bastl 2008, Rektoris et al. 2003).

The frequent hybridization of *P. rotundata* with *P. sylvestris* represents the next serious threat to the *P. rotundata* populations survival, especially at lower altitudes (Businský 1998). For example, the proportion of hybrids (*P.* × *digenea*) is quite high in both Žofinka and Červené blato peatbogs (30-40 %, Rektoris et al. 2003).

Also, several *P. rotundata* stands have recently been destroyed by wind, heavy snowfall, insect infestation and fire in the peatbogs studied [II, III]. Although the destruction of the tree cover induces a rise of the water table [III], which may support *Sphagnum* growth, the combination of the great proportion of hybrids (Rektoris et al. 2003) and the simultaneous low proportion of seedlings makes the future of *P. rotundata* highly threatened, especially in the Třeboň Basin peatbogs.

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TRANSPIRATION OF *PINUS ROTUNDATA* ON A WOODED PEAT BOG IN CENTRAL EUROPE

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Abstract

Transpiration of a central European endemic tree species – *Pinus rotundata* Link – growing on a wooded peat bog in the Třeboň Basin, Czech Republic, was studied in 1999–2000. Transpiration was measured by sap flow techniques (heat field deformation method) on individual trees and scaled up to stand level.

The radial patterns of sap flow density showed narrow peaks in the outer part of the xylem, sapwood accounted for 47–60% of the xylem radius and 72–84 % of the xylem basal area. Adult trees tolerated well both short-term flooding during the growing season and drawdown of the water table to a depth of 60 cm below ground level.

The maximum and mean daily transpiration rates were 3.0 and 1.8 mm per day, and were thus similar to published data for Scots pine. The seasonal total transpiration (25 April – 20 October 2000, 180 days) amounted to 322 mm, or 62 % of the potential evapotranspiration over this period. This canopy transpiration was compensated by 319 mm of precipitation. The difference between the accumulated precipitation and the accumulated transpiration (derived from seasonal sap flow measurements) closely mimicked the seasonal course of the water table.

Key words: bog pine; heat field deformation method; radial profile; sap flow; water balance; water table

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Transpiration of *Pinus rotundata* in a wooded peatbog

Introduction

The presence of trees, especially the genus *Pinus*, is regarded as a natural phenomenon on bogs in continental climates. This contrasts with the naturally treeless oceanic bogs, where the abundance of trees is frequently the result of human activities such as peat cutting, drainage and forest clearance (e.g. Mitchell *et al*. 2001, Cedro and Lamentowicz 2008). Tree growth on bogs is generally poor, largely because the persistently high water table causes inadequate aeration of the rooting zone. Trees are of limited height (up to 10 m), the tree layer is rather sparse. Both the establishment and the growth of tree seedlings is supported by water shortage during more or less pronounced dry summer periods which restrict the growth of *Sphagnum* mosses (Neuhäusl 1972).

Nonetheless, an established tree layer can impact strongly on bog hydrology through intensive transpiration leading to drawdown of the water table (Frankl and Schmeidl 2000). Thus, the estimation of seasonal values of tree transpiration is crucial to water balance

calculations, and there are consequences for the restoration of drained peat bogs (Kučerová *et al*. 2000). The number of studies devoted to evapotranspiration or transpiration in wooded peat bogs (e.g. Humphreys *et al*. 2006) is still very limited compared to the number available for open treeless bogs and fens (Koerselman and Beltman 1988, Lafleur 1990, Lafleur and Roulet 1992). In his summary of evapotranspiration in wooded bogs, Ingram (1983) cited only two studies (Belotserkovskaja 1975, Neuhäusl 1975).

For large trees, transpiration rates can be estimated by micrometeorological (Bowen ratio or eddy-covariance) methods only at sites equipped with tall towers. For a peat bog without special equipment, however, sap flow measurements provide a suitable estimate of canopy transpiration (e.g. Čermák and Kučera 1987, Granier *et al*. 1990, Diawara *et al*. 1991, Čermák *et al*. 1993, Pallardy *et al*. 1995). Several studies of different species (e.g. Čermák *et al*. 1982, Schulze *et al*. 1985, Hatton and Vertessy 1990) have reported that the diurnal course of sap flow rate (measured at breast height) lags behind leaf transpiration, which is considered to depend similarly on radiation. This is important when estimating water storage in trees, but can be neglected when the sap flow method is used to measure the daily sum of whole-tree transpiration (Cienciala *et al*. 1992). Additionally, for time intervals ≥1 day, changes in tree water storage are small and water flow through the sapwood is equal to tree canopy transpiration (Schulze *et al*. 1985). The sap flow rate may almost equal the tree transpiration rate around noon.

Pinus rotundata Link. (bog pine) is a monocormic arborescent subspecies of the *Pinus mugo* complex which dominates central European wooded peat bogs (Businský and Kirschner 2006). Bog pine has a limited geographical distribution in central Europe, which includes parts of Germany, Austria and Poland and is centred in the south-west and south of the Czech Republic (Jalas and Suominen 1973). It grows on flat or slightly convex peat bogs situated in valleys or at the foots of moderate slopes, most frequently at inversion sites in the submontane beech forest belt (Neuhäusl 1972).

Precipitation is the main source of water for the peat bog type known as ‘raised bog’. Most raised bogs originated from *Carex*- or *Phragmites*-dominated stands saturated by upwelling regional water or spring water in the early Holocene. Peat accumulation led to the development of large peat bodies whose vegetated surfaces are now functionally isolated from regional groundwater by thick peat layers with low hydraulic conductivity. The traditional hydrological model (described by Ingram 1978; 1983) proposed that raised bogs were maintained by the impeded dispersal of precipitation, which produces a domed water table (groundwater mound) within the peat. Precipitation infiltrates into the uppermost porous layer (acrotelm), then most of it flows laterally towards the margins of the bog because the deeper peat (catotelm) is perennially saturated due to its low hydraulic conductivity. In such cases, a simple soil water balance may be used to calculate stand transpiration.

The aims of this study were to (i) quantify seasonal tree transpiration in a semi-natural bog pine forest using sap flow measurements; (ii) correlate tree transpiration with meteorological factors; and (iii) compare scaled-up estimates of tree transpiration derived from sap flow measurements on individual trees with estimates based on a simple soil water balance.

Materials and methods

Experimental site

The study site (Červené blato Bog, 48º 52′ N, 14º 48′ E, 465–475 m a.s.l.) is located in the southern part of the Třeboň Biosphere Reserve in the Czech Republic. A detailed description

of the vegetation dynamics of this locality is given by Jeník *et al*. (2002). The Červené blato Bog is a continental raised bog (*sensu* Neuhäusl 1972) or forested bog with natural stands of bog pine (*Pinus rotundata*) and its hybrids with Scots pine (*Pinus* × *digenea* G. Beck). Part of the bog was disturbed by peat cutting in the 19th century.

Mean annual temperature is above 7 ºC in the Třeboň Basin (Přibáň *et al*. 1992) and mean temperature for the growing season (April–September) is about 14 ºC. The climate is rather continental with 600–650 mm of precipitation. Precipitation is considerably higher during the growing season (400–450 mm) than in winter.

The vegetation of the experimental plot was classified as the ass. *Vaccinio uliginosi-Pinetum rotundatae* (Oberdorfer 1934) community. *Pinus rotundata* was the main woody species, whilst *Picea abies* and *Pinus sylvestris* occurred rarely. The shrub layer included many young specimens of *P. rotundata* and less abundant *Frangula alnus* and *Betula pendula*. The herb layer consisted mainly of ericoid species (*Vaccinium myrtillus, V. uliginosum, Ledum palustre*) and graminoids or cyperoids (*Molinia caerulea, Eriophorum vaginatum*). The moss layer included several *Sphagnum* species, *Dicranum* and *Polytrichum* sp. Peat thickness was 5.3 m.

Six experimental trees were selected as being representative of the entire stand on the basis of size, using the technique of quantiles of the total (Čermák and Kučera 1990a) so that each selected tree represented the same fraction of the basal area of the stand. Basic characteristics of the sample trees, such as stem diameter at breast height including the bark (dbh), basal area and crown projected area are summarized in Table 1. The height of the tallest main-canopy tree was almost 15 m.

Table 1. Biometric data for the six measured *Pinus rotundata* trees at the experimental plot on the Červené blato peatbog, Třeboň BR, Czech Republic.

Tree No.	Dbh (cm)	Basal area (cm^2)	Crown projected area (m^2)	Sapwood (% of xylem radius)	Sapwood area (% of xylem basal area)
1	12.6	123	1.41	60.0	84.0
2	14.9	174	1.65	100	100
3	18.0	255	5.53	53.9	78.7
4	20.9	345	5.30	47.3	72.2
5	23.9	449	8.65	48	73.0
6	30.3	720	15.9	49.2	74.2

Measurement and evaluation of sap flow rates

Sap flow was measured using the heat field deformation method (Nadezhdina *et al.* 1998, Nadezhdina *et al*. 2008), which measures deformation of the heat field around a linear heater installed radially in the trunk of the tree. The normal aspect of the heat field at zero sap flow is a symmetrical ellipse, which becomes asymmetrically elongated along the trunk axis as the sap flow rate increases. Deformation of the heat field (as a measure of sap flow) is evaluated as a function of the ratio of two temperature differences, recorded in axial and tangential directions relative to the heater by two pairs of differential thermocouples. Sap flow is calculated from the ratio of the measured temperature gradients, the geometry of the measuring point and the physical properties of the conducting system.

Sap flow was measured in all six of the experimental trees. For routine long-term sap flow monitoring, standard single-point sensors were inserted to a known depth (15 mm) below the cambium from two opposite (western and eastern) sides of the trunk. Multi-point sensors were also installed at a series of locations, in order to investigate the radial pattern of flow and to specify the positions of the standard sensors in this context. Each multi-point sensor needle contained six thermocouples (10 mm apart), and measured flow within the sapwood at six different depths below the cambium. The temperature differences were measured every minute and recorded as means over 15-minute intervals by an EMS-12 data logger (Unilog & Environmental Measuring Systems, Inc., Brno, Czech Republic).

Data for entire trunks were derived by integrating the non-homogenous flow at different sapwood depths over the whole sapwood area (Table 1). The long-term datasets obtained from the single-point sensors were scaled up to tree level on the basis of radial profile measurements made during a single week in May 2000, using the procedure described by Nadezhdina *et al*. (2002). For this, sap flow data measured from both sides of the trunk were averaged. Then the sap flow was expressed per sapwood area corresponding to an individual radial depth (15 mm intervals) by multiplying the appropriate sapwood area by the sap-flow density. We assumed that each measured point was centred on the corresponding sapwood area. Sap flow for the whole tree was integrated by summing individual flows across all sapwood areas in the tree.

Transpiration, measured as sap flow in individual trees, was scaled up to represent a unit area of the entire stand on the basis of a stand inventory. The scaling-up procedure is described in detail by Čermák and Kučera (1987, 1990a). Total daily sap flow was assumed to be equal to total daily transpiration. The best fit for the relationship between daily sap flow rates for individual trees (Q_{wt}) and their basal areas (dbh) was provided by a sigmoidal relationship (Gompertz), applied in the form:

$$Q_{wt}=\{a*\exp[b*\exp(c*dbh)]+d\} \quad (1)$$

The coefficients a, b, c and d were estimated separately for each day for which there was a complete data record. The mean daily transpiration rate for the mean tree of each of a series of tree size (dbh) classes was then calculated using Equation 1. Whole-stand transpiration was calculated by multiplying the number of trees in each class by the daily transpiration for the mean tree of that class, then summing across all classes.

Monitoring of the water balance in the Pinus rotundata stand

Basic meteorological conditions were measured at a standard meteorological screen positioned at a height of 2 m within the experimental plot. Air temperature was measured by a thermistor thermometer connected to an automated data logger (MS16, Fiedler-Magr, Czech Republic). Relative air humidity was measured to an accuracy of ±2% by a thermohydrograph (Novi, Czech Republic); data were logged as hourly values. Additionally, both air temperature and global radiation were measured at a meteorological station in the grounds of the Institute of Botany at Třeboň, 20 km north of the experimental site. Here, global radiation was measured at intervals of ten minutes using a Kipp Zonen radiation sensor mounted on a ten-metre mast, and air temperature with a thermistor thermometer in a standard meteorological screen. There were only minor differences in climatic conditions between the experimental site at the Červené blato Bog and the meteorological station at Třeboň.

Precipitation was recorded by an automated raingauge (SR02, Fiedler-Magr, Czech Republic) installed in a treeless gap in the forest close to the experimental plot.

Daily potential evaporation (PET, expressed in $mm.d^{-1}$) was calculated using the simple equation of Türc (1961), which was positively evaluated by Federer *et al*. (1996):

$$PET = \{[(R_g/0.041868) + 50] * 0.013 * T_a\}/(T_a + 15) \quad (2)$$

where R_g is the daily sum of global radiation ($MJ.m^{-2}.d^{-1}$) and T_a is mean daily air temperature in °C.

The fluctuations of the water table were measured at high temporal resolution (every 15 minutes) using a single submersible pressure transducer (LMP307 sensor, Fiedler-Magr, Czech Republic). Spatial variation of the water table within the experimental plot was estimated manually once a week in a regular network (grid spacing 10 m) of 16 dipwells (1.5 m long PVC pipe, 5 cm diameter). Soil moisture content was measured using VIRRIB sensors (Amet, Czech Republic) at three different depths (15, 25, and 35 cm) and estimated manually once a week.

Estimation of evapotranspiration from the simple soil water balance

Simple soil water balance is based on a water budget for the Dun Moss raised bog published by Ingram (1982):

$$P - E - U - G - \Delta W = 0 \quad (3)$$

in which all terms are flux densities except ΔW and where P = precipitation, E = evapotranspiration, U = lateral discharge, G = vertical discharge through the catotelm and ΔW = storage.

Our experimental plot had an almost impermeable layer of highly decomposed peat at 65 cm depth (unpublished data) therefore G was suppossed to be almost zero. Precipitation (P) either infiltrated to become shallow groundwater and increase soil water content (ΔW), or was laterally discharged (U). According to our long-term unpublished data, lateral discharge (U) ceased when the water table was drawn down to 15 cm below the ground surface at the beginning of the summer period of water deficit, and did not resume until the water table returned to almost the same position late in the growing season. As we can assume zero change in soil water storage between times when the water table is in the same position, stand evapotranspiration is approximately equal to precipitation for periods with zero discharge and the same water table. For appropriate periods the modified soil water balance could be written as

$$P - E = 0 \quad (4)$$

A suitable period for such a calculation was identified as 01 April to 07 August 2000.

Results

Meteorological conditions during this study

Comparison with long-term seasonal data indicated that the weather conditions during the 1999 and 2000 growing seasons were atypical. Climatic water deficit was quite high in some months of both years (64 mm in August 1999; 69 mm in June and 92 mm in July 2000). In 2000, July was cooler and both June and August were much warmer than average. Vapour pressure deficit was temporarily high in the third part of both June and August 2000 (daily maximum 3.8 kPa).

During warmer and drier periods, PET calculated according to Türc (1961) reached 5.1–5.7 mm.d^{-1} and the calculated total for the 2000 growing period (180 days) was 519 mm.

Radial profiles of sap flow

In five of the sample trees, the radial patterns of sap flow density showed narrow peaks in the outer part of the xylem. Splaining curves fitted the measured points with r^2 = 0.98, thus exactly characterising the patterns. In these trees, sapwood accounted for 47–60% of the xylem radius and 72–84 % of the xylem basal area (Table 1 and Figure 1). The exception was Sample Tree 2, where the whole cross-sectional area of the xylem was conducting, there was a wide peak of sap flow encompassing 70% of R_{xyl} (Figure 1), and curve fitting gave r^2 = 0.90. The radial position chosen for the standard sensors (15 mm below the cambium as recommended by Nadezhdina *et al*. 2002) coincided approximately with the maximum sap flow density in all of the sample trees.

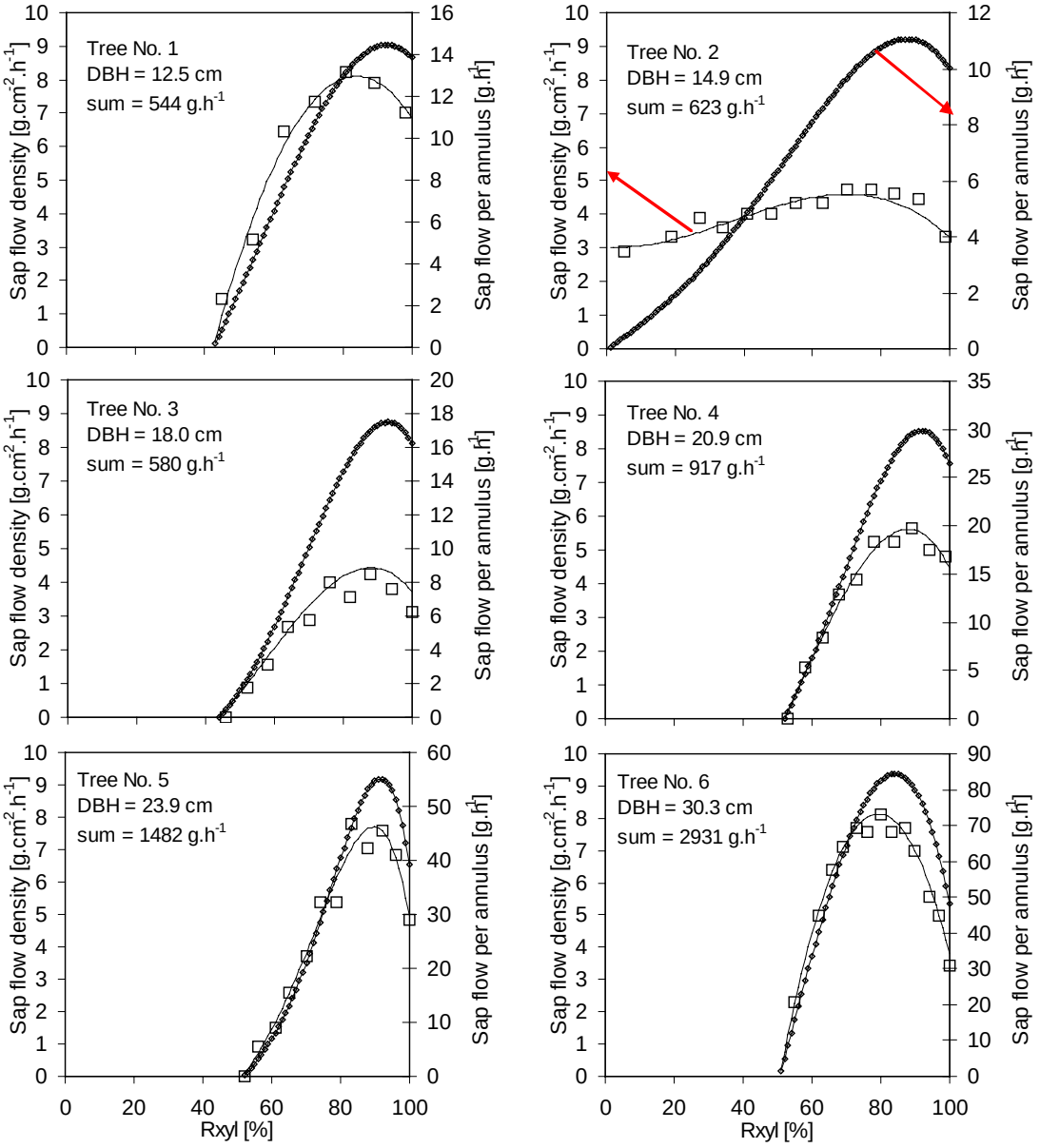

Fig. 1 Radial patterns of sap flow in the trunks of six *Pinus rotundata* sample trees growing within the experimental plot on the Červené blato Bog. Sap flow is expressed per unit area of conducting wood (measured data) and per unit cross-sectional area of the annulus of conducting wood (calculated data with step of 2% of xylem radius). Sap flow in all of the annuli was summed to give total flow for the whole tree during the relevant part of the day

Diurnal courses and maxima of sap flow in individual trees

There was a small time lag between the respective rises in radiation and sap flow in the morning. During cloudless weather, the sap flow rate in all of the sample trees started to increase almost simultaneously with the development of an air vapour pressure deficit (VPD) above the vegetation surface (Figure 2). The maximum values were measured around noon, when irradiation also peaked. No noon depressions of sap flow/transpiration were recorded at any time during the study period, except when there was a parallel decrease in global radiation (there was frequently an increase in cloudiness around midday on otherwise sunny days). After the evening decrease of global radiation, sap flow continued at a low and decreasing rate until late at night. The diurnal pattern of sap flow differed slightly between individual sample trees due to the different shapes of their crowns and local shading (Figure 2b), but their relative sap flow rates did not change significantly during the study period.

Sap flow was closely linked to incident radiation and responded sensitively to changes in irradiance caused by passing clouds, to precipitation (mark A in Figure 2b), and to even small increases in VPD during the night (mark B in Figure 2b). During periods of successive clear hot days, the maximum daily sap flow rate was mostly controlled by incident radiation and did not reflect the progressively higher maximum values of VPD recorded around noon (cf. Figure 2a and Figure 2b).

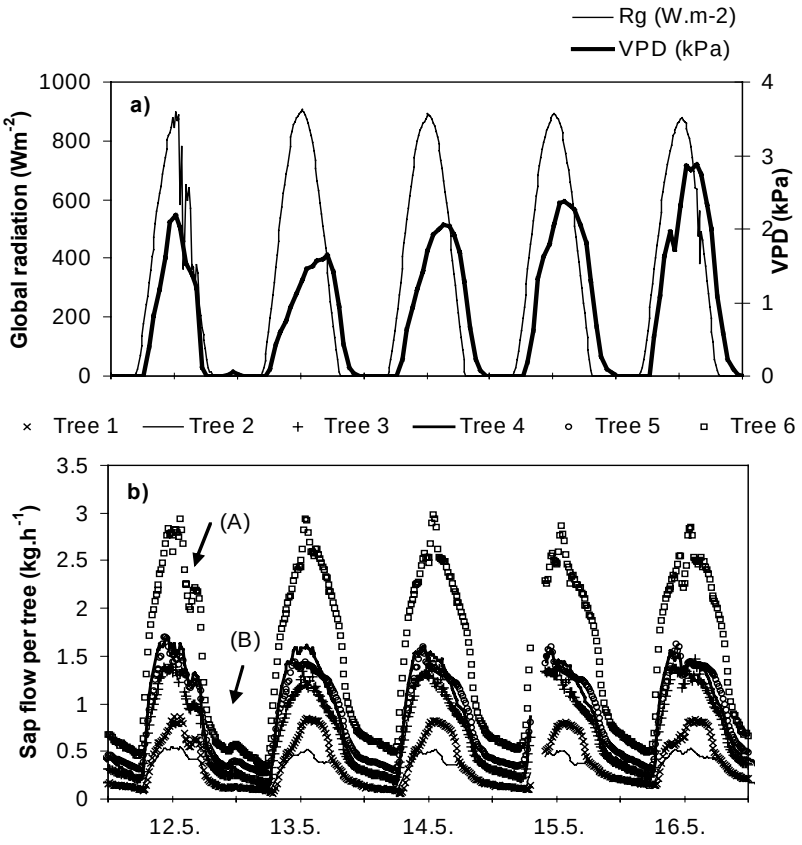

Fig. 2 Variation of global radiation and vapour pressure deficit (a) and variation of sap flow between individuals (b) in six *Pinus rotundata* trees during a period with high evaporative demand (12–16 May 2000). Sap flows responded sensitively to clouds and precipitation (mark A), and to even small increases in vapour pressure deficit during the night (mark B)

Maximum sap flow rates calculated as means of the actual field measurements for the three days with the highest sap flow rates are given in Table 2. The maximum daily transpiration of the largest sample tree (dbh = 30.3 cm) was more than 48 litres per day or 3 $mm.d^{-1}$ per crown projected area during cloudless days with high evaporative demand (PET approximately 5.5 $mm.d^{-1}$). Both the maximum hourly sap flow rates and the maximum daily totals were higher for larger trees. However, maximum daily totals of sap flow expressed per unit of crown projection were higher for smaller trees, suggesting more efficient utilization of available space to take advantage of incoming solar energy by smaller trees.

Table 2. Maximum sap flow rate (mean of three days with the highest seasonal sap flow rate) in *Pinus rotundata* sample trees of different sizes, calculated in various units.

	Sample tree no. (dbh in cm)	**Sap flow per sample tree** (kg)	**Sap flow per basal area** ($kg.m^{-2}$)	**Sap flow per crown projection** ($kg.m^{-2}$)=mm
Daily total maximum	1 (12.6)	11.9	965	8.39
	2 (14.9)	10.0	571	6.04
	3 (18.0)	24.4	958	4.41
	4 (20.9)	26.3	768	4.96
	5 (23.9)	26.1	581	3.01
	6 (30.3)	48.6	675	3.06
Daily maximum per hour	1 (12.5)	1.48	120	1.05
	2 (14.9)	0.86	49	0.52
	3 (18.0)	2.95	116	0.53
	4 (20.9)	2.98	87	0.56
	5 (23.9)	2.30	51	0.27
	6 (30.3)	8.40	117	0.53

Upscaling from sample trees to forest stand

The mean daily transpiration of the largest (dbh 31–33cm) and smallest (dbh 5–7 cm) trees was 33.3 $kg.tree^{-1}$ and 1.2 $kg.tree^{-1}$ respectively (Figure 3a). Trees with medium dbh (17–23 cm) and mean daily transpiration represented the most important functional part of the stand, accounting for 60% of the whole-stand transpiration (Figure 3b). The largest trees with the highest daily transpiration per tree contributed only marginally to whole-stand transpiration (7% of the whole-stand transpiration from three dbh classes 27–33 cm), due to their low frequency.

Transpiration of the Pinus rotundata stand

Stand transpiration was high during cloudless weather in different summer months (e.g. June 2000, August 2000). The mean of the three consecutive clear-sky days was about 2.9 $mm.d^{-1}$, and the seasonal maximum of 3.0 $mm.d^{-1}$ was observed on 22 June 2000 (PET 5.5 mm). Stand transpiration was lower in spring and autumn, but remained an important component of the stand water balance up to the end of October (Table 3).

The daily canopy transpiration rate, as measured by the sap flow technique, was closely correlated with potential evapotranspiration (Figure 4a, r^2=0.86). This allowed the construction of a regression equation so that extrapolated data could be calculated for days when sap flow

measurements were missing from the data record. The sum of PET from 25 April to 20 October 2000 was 519 mm. The total seasonal canopy transpiration for the same period (measured as sap flow) was 322 mm, i.e. 62% of PET. The seasonal mean canopy transpiration was 1.8 $mm.d^{-1}$ (Table 3).

The evapotranspiration calculated from the simple water balance was 247.6 mm (i.e. 1.9 $mm.d^{-1}$) for the period 01 April to 07 August 2000, and was slightly lower than canopy transpiration, calculated by scaling-up of the sap flow data, for the same period (257.8 mm, i.e. 2.0 $mm.d^{-1}$).

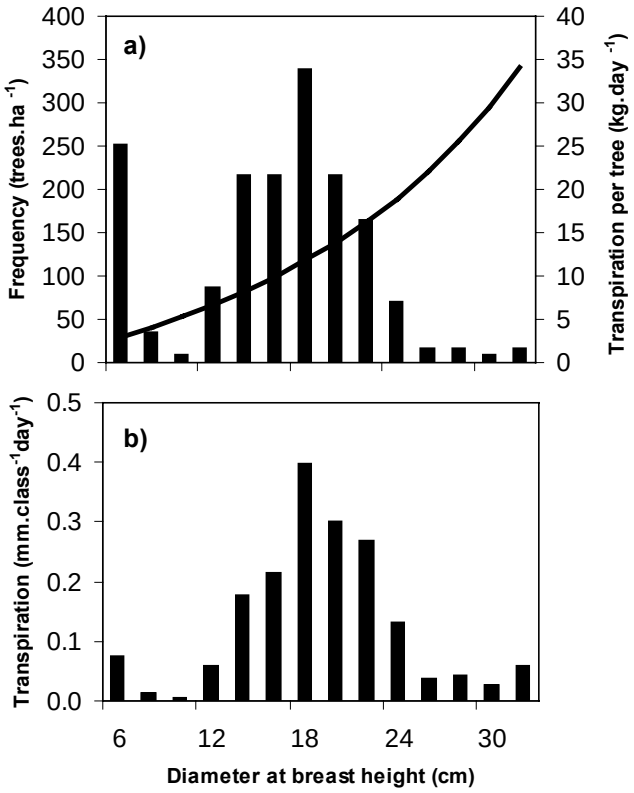

Fig. 3 Scaling of transpiration from individual sample trees to various dbh classes and to the experimental stand: a) Numbers of trees in dbh classes (left y-axis, histogram) and mean daily transpiration of mean trees of dbh classes calculated from the scaling curve (right y-axis), and b) Mean daily transpiration of all trees within each class (the mean daily transpiration obtained by summing the values for all classes was 1.8 $mm.day^{-1}$)

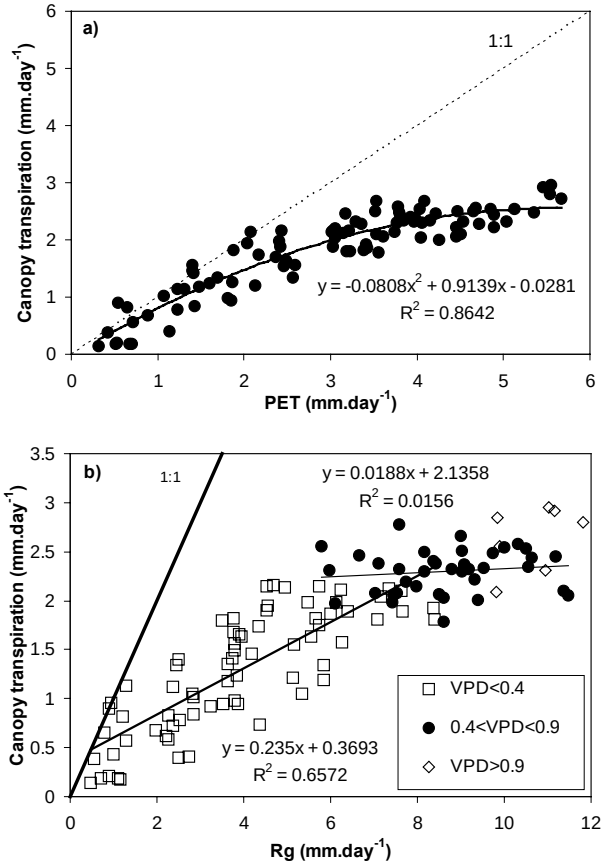

Fig. 4 a) Relationship of *Pinus rotundata* canopy transpiration to daily totals of potential evapotranspiration (PET) from April to October 2000, **b)** relationship of canopy transpiration to daily totals of global radiation (Rg) classified according to the different mean daily vapoure pressure deficit values

Table 3. Annual and monthly means (± s.d.) of *Pinus rotundata* bog forest canopy transpiration and potential evapotranspiration (PET). The annual mean and total values apply to the 180-day period from 25 April to 20 October 2000.

Month	Mean PET [mm]	Mean canopy transpiration [mm.d^{-1}]	Stand T/PET [%]
August 1999	3.0±0.9	2.1±0.5	74.0
September 1999	2.3±0.8	1.7±0.5	77.8
October 1999	0.9±0.4	1.0±0.3	118
May 2000	3.4±1.0	2.0±0.4	61.5
June 2000	4.1±1.2	2.3±0.4	57.6
July 2000	2.7±1.0	1.8±0.5	67.4
August 2000	3.5±1.0	2.1±0.4	62.8
September 2000	1.9±0.7	1.4±0.4	73.6
October 2000	1.0±0.5	0.8±0.3	81.3
Mean 2000	2.9±1.4	1.8±0.6	
Sum 2000	519	321.5	62.0

Transpiration in relation to meteorological factors

Scaled-up daily canopy transpiration was non-linearly related to PET (Figure 4a, $r^2 = 0.86$), demonstrating a substantial limitation of transpiration under high evaporative demand. VPD exerted a stronger influence than global radiation (Rg) on the non-linearity of this relationship (Figure 4b). Therefore, the correlation of canopy transpiration with Rg was significant only when VPD was below a threshold value of 0.4 kPa (Figure 4b, $r^2 = 0.66$). For higher VPD values, canopy transpiration remained almost constant, regardless of any further increase in global radiation or VPD (Figure 4b).

Transpiration in relation to soil conditions

Scaled-up sap flow standardized by PET did not correlate with the volumetric soil water content ($r^2 = 0.02$, Figure 5) during the long periods of high precipitation deficit in the summer of 2000. However, both canopy transpiration and precipitation were reflected in the seasonal fluctuations of the water table and soil water content (Figure 6). The pronounced changes in water table position clearly followed the calculated difference (in mm) between the accumulated precipitation and the accumulated transpiration ($D = P - T$) (Figure 6).

Heavy rain (54 mm.day^{-1}, total 87.4 mm for 1 week) occurred after a fairly long dry period at the beginning of August 2000, raising the water table abruptly to its seasonal maximum position (15.4 cm below ground level). Observation of windthrown (uprooted) trees nearby indicated that the root systems of standing trees were approximately 15–30 cm below the surface, so that most of them should have been flooded for the following 5 days. No abrupt diurnal changes in sap flow were observed immediately after the rainy period. Moreover, the tree transpiration rates were very high due to the high evaporative demand from 10 August, suggesting that no important damage to roots was caused by this short period of flooding, even though parts of the root systems were probably still flooded (Figure 7).

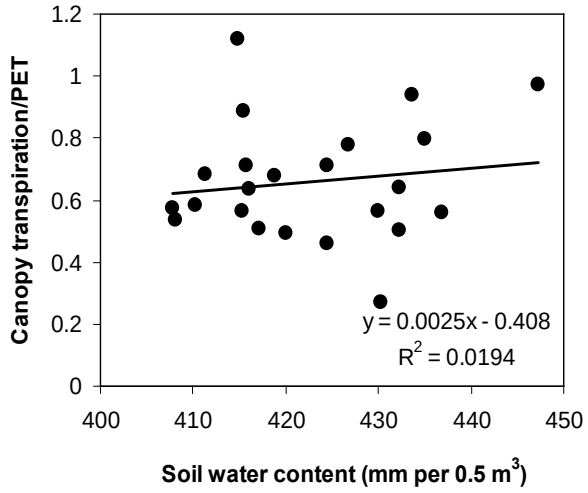

Fig. 5 Daily canopy transpiration (standardized by potential evapotranspiration) in relation to volumetric soil moisture content

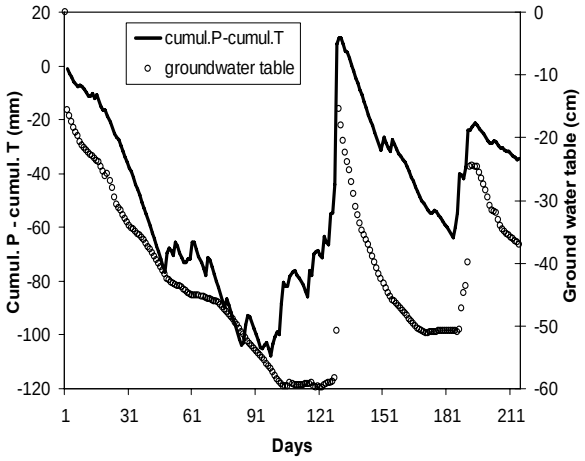

Fig. 6 Seasonal course of the measured water table level (GWT) and of the calculated difference between cumulative precipitation (ΣP) and cumulative canopy transpiration (ΣT) measured by the sap flow method for the growing season of 2000

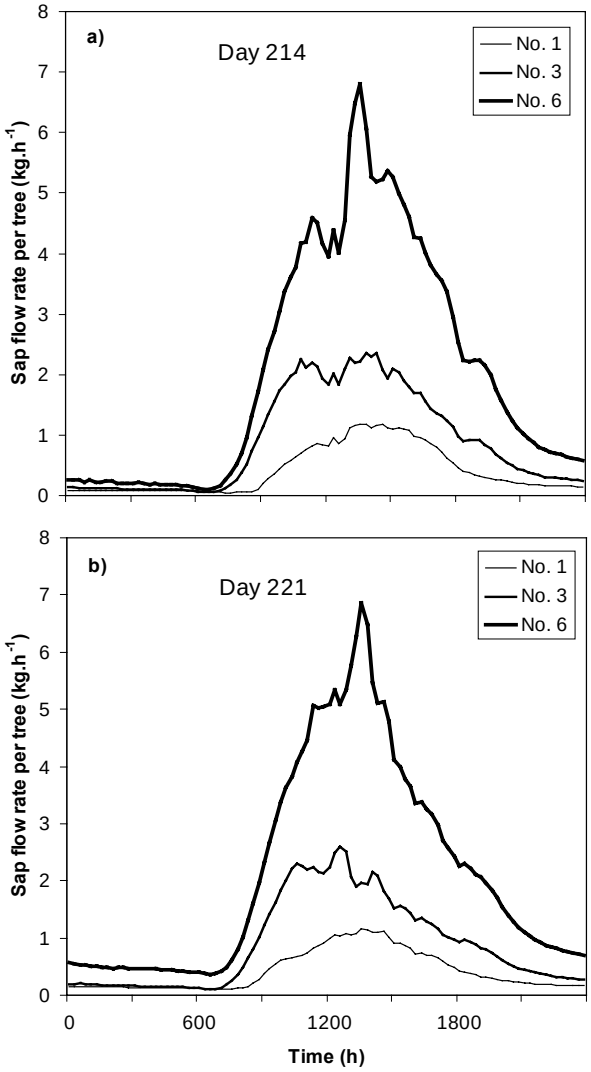

Fig. 7 Individual variation of sap flow in three *Pinus rotundata* trees before flooding of the rooting zone (a, Day 214', 01 August 2000) and after that (b, Day 221', 10 August 2000). Both days had similar potential evapotranspiration and vapoure pressure deficit, but very different water table depth (60 cm and 20 cm below ground level, respectively)

Discussion

Radial sap flow patterns

The variation in radial patterns of *Pinus rotundata* sap flow density observed in our study is similar to that found in Scots pine on sandy soils in Belgium, where peak values occurred at 85–95% of the stem radius and total sapwood depth was 60% of the xylem radius (Čermák and Nadezhdina 1998, Nadezhdina *et al*. 2002). A relatively large sapwood area with a single radial peak of sap flow (usually around the middle sapwood) has also been reported for other temperate coniferous species (e.g. for spruce by Čermák *et al*. 1992), while various patterns of

radial flow have been observed in broadleaved species (Phillips *et al*. 1996, Čermák and Nadezhdina 1998, Lu *et al*. 2000, Jimenéz *et al*. 2000).

The different radial pattern of sap flow density found in Sample Tree 2 (Figure 1) may be associated with its small dbh, as the radial pattern of sap flow may change with tree size and age. Conducting sapwood occupies the whole xylem radius in young *Quercus pubescens* trees, and decreases its percentage gradually with age (Čermák and Nadezhdina 1998). Low sap flow rates with little variation along the stem radius have also been reported in shade-suppressed laurel trees, in contrast to the high sap flow rates with typical peaks, usually in the outer sapwood layers, exhibited by dominant trees (Jimenéz *et al*. 1996). Additionally, damage to stems or surface roots can result in a significant decrease in sap flow rate in the outer xylem layers (Jimenéz *et al*. 2000).

Maximum sap flow rates

The highest hourly sap flow rates were measured in all of the sample trees during the second half of August 2000, probably as a result of higher LAI reflecting the full development of current-year needle foliage in late summer. Transpiration (and photosynthesis) could occur in both current-year and one-year-old needles at this time of year. However, the maximum hourly sap flow rate did not correlate with the maximum daily sap flow (or transpiration) rate due to the shorter duration of daytime radiation in August compared with June, when most of the highest daily totals were measured.

Maximum daily transpiration for the largest sample tree (dbh = 30.3 cm) was over 48 $kg.d^{-1}$ on cloudless days with high evaporative demand. Considering the relatively small height of *P. rotundata* trees (15 m maximum), their seasonal and daily transpiration rates were high compared with published rates for *P. sylvestris* (c.f. Verbeeck 2007). *P. rotundata* has a longer and denser crown than *P. sylvestris*, probably with more foliage, which could offset the effect of its limited height.

Canopy transpiration

The seasonal transpiration observed for the *P. rotundata* bog forest was probably close to its maximum, as there was frequent cloudless weather and sufficient water supply during the period of measurements.

No direct restriction of tree transpiration (by partial closure of stomata causing a decrease in sap flow rate in the middle of the day) due to soil drought was observed in either year of the study, even when the water table declined to 60 cm below ground level. Nevertheless, although the trees were well supplied with water during the whole season, the canopy transpiration amounted to only 62% of the PET. Additionally, the ratio of tree T/PET was consistently higher in autumn than in summer (Table 3), indicating limited sap flow rates under conditions of generally high VPD in summer. Diurnal sap flow rates during the period of high evaporative demand and non-limited soil water supply showed a similar limitation of transpiration (Figure 2) – the higher VPD was not reflected by an increase in transpiration rate, which rather remained at a certain (probably maximum) rate for several days. This indicates that there was an upper limit to transpiration in the investigated trees, even when the soil water supply was not limiting.

Similarly, Köstner (2001) reported that transpiration in several central European forests, studied using the scaled-up sap flow and eddy correlation methods, was limited more often by low canopy conductance on days of high VPD than by periodic soil drought. Also, a decline in surface conductance with increasing VPD indicating physiological restrictions to transpiration, particularly in peatlands with woody vegetation, was reported by Humphreys *et*

al. (2006). Water transport efficiency is likely to limit the rate of transpiration in trees, especially in conifers with narrow tracheids. However, stomatal conductance may also decline in response to increasing VPD of the air (Lambers *et al.* 1998). Water loss is therefore restricted when dry air is likely to imposse water stress (Schulze 1986) and transpiration could be constant over a range of VPDs. Obversely the limitation of tree transpiration by severe soil drought is quite rare and restricted to extreme soil or climatic conditions (e.g. Poyatos *et al*. 2005, Nadezhdina *et al*. 2007).

We used only six experimental trees, supposing this number to be sufficient for up-scaling because the experimental plot was quite homogeneous and almost all dbh classes were represented in our sample. However, the smallest trees (dbh 5–7 cm), which were present in high numbers (252 trees per ha), were outside the measurement range of the sap-flow method employed. These smallest trees were the most shaded and suppressed individuals, with limited income of solar energy. Also, they probably hardly survive due to strong competition, as indicated by their highly suppressed growth (very narrow annual rings, person. observ.). Therefore, only a small error is likely to be introduced by estimating daily sap flow rates for this class, at approximately 2% of the total canopy transpiration.

Comparison with published measurements

Direct estimates of transpiration for *Pinus rotundata* (or even *Pinus mugo* agg.) are completely absent from the literature. However, the transpiration of the *P. rotundata* bog forest can be compared with that of either boreal coniferous forests or wooded bogs. We report a seasonal canopy transpiration of 322 mm, with a maximum of 3.0 $mm.d^{-1}$ and daily mean of 1.8 $mm.d^{-1}$ (Table 3). Similar values of seasonal stand transpiration were estimated by Cienciala *et al*. (1994) for spruce forests in SE Sweden (mean daily transpiration 1.6 mm, seasonal total 325 mm over 190 days, ratio of seasonal totals of actual and potential transpiration 68% where PET=480 mm). There are few comparable estimates of transpiration for Scots pine of similar structure, climate and growing season. Meiresonne *et al.* (2003) reported mean daily transpiration (derived from sap flow measurements) of 1.3 $mm.d^{-1}$ for a 70-year-old Scots pine stand in Belgium during July-August 1997. The main water balance components for a Scots pine stand (*Pinus sylvestris* L.) growing on a sandy soil with shallow water table (0.80 m deep in spring) were estimated by Vincke and Thiry (2008). From May to November, pine transpiration never exceeded 1.8 $mm.d^{-1}$ and reached a total of 176.4 mm, which amounted to 25% of potential evapotranspiration. Therefore, the canopy transpiration values that we obtained for *Pinus rotundata* are similar to those available for many coniferous forests in Europe (cf. Köstner 2001; Roberts 2007).

Tolerance of soil inundation

In many species of forest trees, soil inundation is followed by rapid stomatal closure and this may cause a substantial decline in transpiration (e.g. Kozlowski *et al*. 1991). Čermák and Kučera (1990b) reported a 60% fall in transpiration for an old spruce stand, persisting until the end of the growing season, as a result of heavy rainfall (150 mm in 3 days) which reduced soil aeration. However, the transpiration rate of *P. rotundata* trees was not reduced after pronounced increase of water table; indeed, transpiration rates were close to the maximum values. Therefore, the adult trees of the species can tolerate short-term soil flooding, even during the growing season. Probably superficial roots, concentrated in very porous superficial peat could supply the trees with enough oxygen.

Up-scaling sap flow versus soil water budget

The independent estimate of stand level evapotranspiration (simple soil water budget) was very similar to the estimate derived by scaling up the sap flow measurements. For the period 01 April to 07 August 2000, the value obtained from the soil water budget was 247.6 mm (i.e. 1.9 $mm.d^{-1}$) and from the scaled-up sap flow data 257.8 mm (i.e. 2.0 $mm.d^{-1}$). This means that tree transpiration accounts for almost 100% of the whole-stand evapotranspiration and that the (evapo)transpiration of both the herb and the moss layer may be almost negligible. In contrast, Grelle *et al*. (1997) estimated the understorey contribution at 15% of total evapotranspiration for a 50-year-old boreal forest in Sweden, and a similar understorey evapotranspiration was estimated by Vincke and Thiry (2008) for a Scots pine forest on sandy soil (18–20% of the stand water use). This discrepancy may be partially attributable to the uptake by vegetation of water from the unsaturated layer above the water table, which was not included in the simple soil water balance calculations. Additionally, soil water budget estimates may be erroneous under conditions of severe surface dryness and after rainfall events (Wilson and Baldocchi 2001).

Nevertheless, the dominant understorey species in our experimental plot was *Vaccinium myrtillus*. This deciduous ericoid shrub had probably very low transpiration during April because leaf expansion is not complete until the middle of May. Also, the soil was completely covered by a moss layer, which hampered soil evaporation. Evaporation from the moss layer may be limited to times of maximum water saturation in early April and/or after heavy rainfall. Moreover, Heijmans *et al*. (2004) reported that evaporation from a moss carpet in boreal forest was lower (0.3 $mm.d^{-1}$) than on open bog (1.5 $mm.d^{-1}$), where wind was the main driving force for evaporation from *Sphagnum*. Therefore we conclude that the scaled-up tree transpiration data provide a reliable indication of (evapo)transpiration from this central European bog forest.

Isolated peat bogs in central Europe can be regarded as islands in the landscape, in terms of both biodiversity (Nekola 1998) and energy/matter budgets (water, energy and carbon fluxes). A peat bog of limited size may be influenced by the advection of dry air from the surrounding drained cultural landscape. The limited transpiration of *Pinus rotundata* under conditions of high VPD (or advection of dry air) could be advantageous in maintaining a suitable water balance for a peat bog. In contrast, several wetland broadleaved trees and shrubs like *Alnus glutinosa*, *Frangula alnus*, *Betula* sp. and *Salix* sp. can transpire at high rates even when VPD is high (Čermák *et al*. 1984, Přibáň and Ondok 1986). Thus, long-term changes in tree composition leading towards domination of a peat bog by these broadleaved trees/shrubs (e.g. Kučerová *et al*. 2000) could accelerate water table drawdown and cause further vegetation changes.

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DISTURBANCES ON A WOODED RAISED BOG – HOW WINDTHROW, BARK BEETLE AND FIRE AFFECT VEGETATION AND SOIL WATER QUALITY?

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Abstract

A *Pinus rotundata*-dominated peatbog (Žofinka Nature Reserve) in the Třeboň Basin, Czech Republic, was affected by 'natural' disturbances: wind damage (in 1984), followed by a bark beetle attack, and fire (1994; 2000). Phytosociological relevés were used to document vegetation. Soil water chemistry was compared in three differently affected stands: (i) an undisturbed *Pinus rotundata* bog forest, (ii) a windthrow–bark beetle affected stand and (iii) a site burned by wildfire in 2000.

The species composition of the windthrow–bark beetle affected sites and the undisturbed *P. rotundata* bog forest differed mainly in the shrub and tree layers. Burned sites were partly colonized by anemochorous species (e.g. *Taraxacum* sp. div.) that disappeared within two or three years after colonization. Bare peat was colonized by bryophytes (e.g. *Marchantia polymorpha* and *Funaria hygrometrica*) typical of the disturbed sites, and by *Polytrichum* sp. div. and *Aulacomnium palustre*. Most plant species characteristic of the *P. rotundata* bog forest occurred at the burned sites eight years after the fire, but in different abundances. The edificator of the former community – *P. rotundata* – was mostly absent. Compared with windthrow followed by the bark beetle attack, fire promoted rapid expansion of *Molinia caerulea*.

Soil water in both the undisturbed *P. rotundata* bog forest and the windthrow–bark beetle affected sites had a similar composition: very low pH values, high P concentrations, low concentrations of cations (Ca^{2+}, Mg^{2+} and K^{+}) and inorganic nitrogen. The concentrations of soluble reactive phosphorus (SRP) and NH_4^{+}-N were negatively correlated with the groundwater table.

Total P, SRP and NH_4^{+}-N concentrations in the soil water at the burned site were by one order of magnitude higher than those in the *P. rotundata* bog forest, while concentrations of K^{+}, Mg^{2+} and Ca^{2+} were only about two times higher. High concentrations of P and N in the soil water found three years after the fire indicated a long-term elevated nutrient content in the soil water.

Keywords: Czech Republic, Groundwater chemistry, Nitrogen, Phosphorus, *Pinus rotundata,* Post-fire succession

Introduction

Windstorms, bark beetle infestation and fires are supposed as the natural processes in the long-term development of the northern taiga ecosystem (Wein & MacLean 1983, Frelich & Reich 1995). Understorey plant species of boreal forests are well adapted to frequent disturbances (Rowe 1983). However, such disturbances could have a strong effect on species diversity and ecosystem functions especially in size-limited protected areas. Nevertheless, natural long-term succession of wind- or fire-damaged forests was only rarely reported from Central Europe (cf. Fischer et al. 2002, Jonášová & Prach 2004).

The Central European *Pinus rotundata*-dominated bog communities (*Pino rotundatae-Sphagnetum* Kästner & Flössner 1933 corr. Neuhäusl 1972) resemble the northern taiga

ecosystem (Jeník et al. 2002, for distribution see Neuhäusl 1972). The community occurs only as a relict on deep peatbogs up to 1000 m a.s.l (Businský 1998).

Windthrows create gaps that increase light and release other resources for understorey trees, herbs and seedling growth (Mladenoff 1987). Both wind and insect infestations can alter competitive relationships between plants (i) directly through selective mortality, and (ii) indirectly because defoliation triggers carbon and nutrient release (Beudert 1999). Mosses without roots are mostly isolated from the groundwater table in *P. rotundata*-dominated peatbogs. This isolation occurs because of a regular drop in the groundwater table in summer (lowest groundwater table -65 cm below ground in late summer) and because the groundwater table never reaches the soil surface in this community (highest level -15 cm below ground in early spring, Kučerová et al. 2000). Therefore, precipitation remains the main source of nutrients for mosses. Obversely, vascular plants (ericoid shrubs, trees) could effectively absorb soil water nutrients through their roots. Therefore, any disturbance that increases the soil water nutrient concentration could change the competition pattern between vascular plants and mosses.

Fire induces drastic changes in the vegetation cover and the environment (e.g. changes in soil-moisture content, microclimate near the ground, irradiance). Burning could lead to increased nutrient levels, especially to extremely high peak concentrations for both P and K because of surface deposit of plant ash (Tallis 1983). As a result, "nitrophilous" species or weedy plants dominate the initial recolonization stage. However, in a paleoecological study Kuhry (1994) suggested that the effect of local peat surface fires on vegetation cover is only short-term. Prefire conditions usually return within decades after the burning, and long-term vegetation development is not affected. It can be hypothesized that any nutrients released by burning are quickly leached out from permanently wet peatbogs.

In the 1970s the Žofinka peatbog was recognized as a well-preserved locality of the *P. rotundata* bog forest (Kučera 1977). However, severe windthrows (in 1984) and a follow-up attack of insects destroyed most of the tree layer (Liška et al. 1989). Further, two small fires affected the peatbog in 1994 and 2000. Approximately 3 ha were destroyed during each fire. Therefore, the locality offered an excellent opportunity to study the effects of different disturbance factors on initially similar sites. In this study, natural post-fire succession on a wooded raised bog was reported for the first time from Central Europe.

The objectives of this study were (i) to describe the post-fire colonization in the *P. rotundata*-dominated peatbog, and (ii) to compare vegetation and soil water quality at three differently disturbed sites on the peatbog – a burned site, a windthrow–bark beetle affected site, and an undisturbed *P. rotundata* bog forest.

Material and methods

Nomenclature

Kubát et al. (2002), Kučera & Váňa (2003)

Study site

The study site (N 48°49', E 14°53', 470–475 m a.s.l.) is located in the southern part of the Třeboň Biosphere Reserve in the Czech Republic, 22 km south of Třeboň (Fig. 1). The Žofinka peatbog (130 ha) is a continental raised bog (sensu Neuhäusl 1972) or treed bog. The tree layer consisted of uneven-aged stands of *Pinus rotundata* (monocormic species from the *Pinus mugo* complex, Businský 1998), with small admixture of *Pinus sylvestris* (max. 10%). The herb layer included ericoid dwarf shrubs (*Ledum palustre, Vaccinium myrtillus, V. vitis-idaea* and *V. uliginosum*) and the moss layer was dominated especially by *Sphagnum* species

(e.g. *S. fallax* and *S. capillifolium*), *Dicranum polysetum, Polytrichum formosum* and *Pleurozium schreberi.*

Severe windthrow (in 1984) disturbed the most valuable stands of the *P. rotundata* bog forest. Many small- and large-scale windthrows became a food basis for the next bark beetle infestation. Liška et al. (1989) reported the large-scale attack of different species of wood engraver on living *P. rotundata* trees in 1988. The former *P. rotundata* bog forest persisted only in fragments. Further, two small fires affected the peatbog in 1994 and in 2000.

The Žofinka peatbog is situated in a shallow depression of cretaceous bedrock. The bedrock is made up of sediments of the Klikov series – sand, clay and clayey sand (Koroš et al. 1998) and is very acidic and poor in nutrients. According to Koroš et al. (1998), the peatbog originated from a gradual local subsidence of the cretaceous bedrock, consequently followed by a local increase in the groundwater table. The bog surface is flat and maximum peat depth is about 4 m. Two deep drainage channels demarcate the Reserve in the NW and NE. Two shallow drainage ditches (ca. 0.5 m deep), penetrate the central part of the bog in the NW–SE direction.

Mean annual temperature is 7.8 °C in the Třeboň Basin (Přibáň et al. 1992) and mean temperature in the vegetation period (April–September) is about 14 °C. Total annual precipitation is about 600–650 mm. Precipitation in summer is appreciably higher (400–450 mm) than in winter.

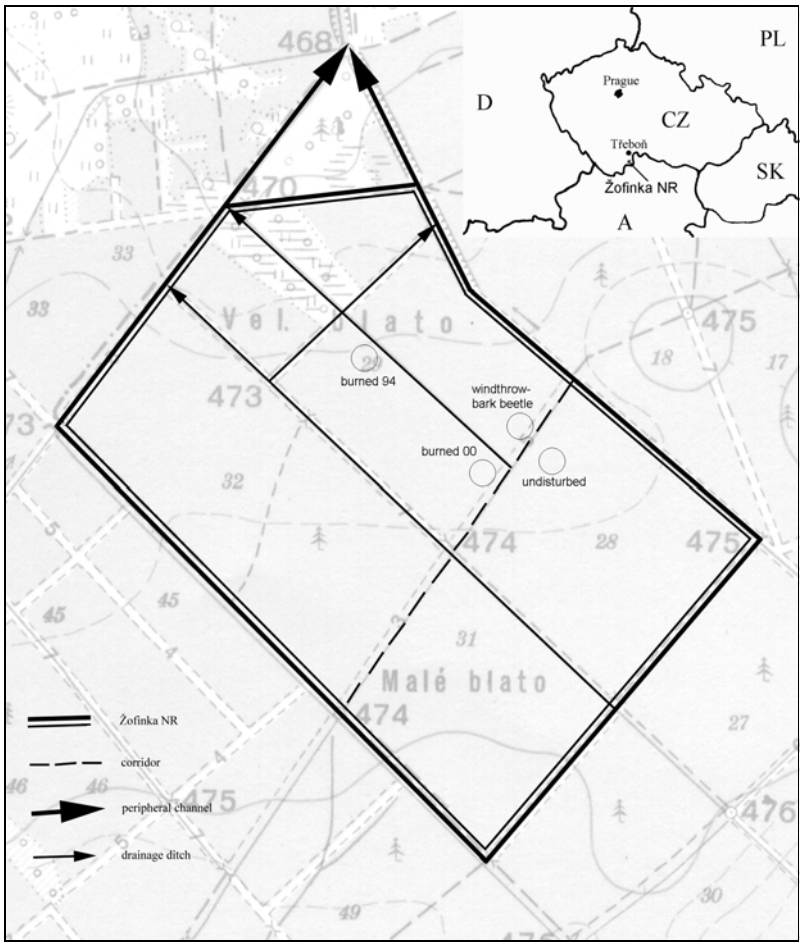

Fig. 1. Localization of plots burned in 1994 (burned 94), burned in 2000 (burned 00), windthrow-bark beetle affected (windthrow-bark beetle), and plots in undisturbed *P. rotundata* forest (undisturbed) in the Žofinka peatbog. For localization of the study site in Central Europe see the inset diagram.

Vegetation data sampling

The following sampling sites were chosen for the comparison of vegetation and soil water chemistry: (i) an undisturbed *P. rotundata* bog forest site as control, (ii) the windthrow–bark beetle affected site, and (iii) the burned sites (from 1994 and 2000, respectively). All sampling sites were situated in the central part of the reserve. They all belonged to the same vegetation type – the *P. rotundata* bog forest – until the disturbances took place. According to terrain slope and hydrological situation, the water and nutrient exchange among the experimental plots were possible only in the direction from the undisturbed plots towards the burned plots (cf. Fig. 1).

Sampling plots (Table 1) were located in a subjective

way to best represent the type of disturbance. At each plot, vegetation was recorded using the phytosociological relevé method. The nine-degree Braun-Blanquet cover scale as modified by van der Maarel (1979) was used.

Chemical analysis

Test water sampling was made in all studied sites during 2001 (three samples in each site, incl. site burned in 1994). In June 2002 new dipwells (perforated PVC pipes, 1 m long, diameter 50 mm) were inserted into the peat to a depth of up to 70 cm in the following sampling sites: (i) the undisturbed *P. rotundata* bog forest site, (ii) the windthrow–bark beetle affected site, and (iii) the site burned in 2000. In each sampling site three dipwells were installed at a 10-m distance from the permanent plots. All dipwells were covered with small caps to prevent water contamination from litter or insects. Before the first sampling at the beginning of the growing season, all dipwells were emptied to clean them sufficiently. Two 100-ml samples were taken from the top of the groundwater table. After sampling the dipwells were emptied again. Groundwater table depths were measured before the water sampling. The sampling interval was ca 4 weeks during the growing season. In total nine samples were taken from each dipwell (four samples during 2002 and next five in 2003).

Water samples were stored in a refrigerator, while pH and conductivity were measured at 20 °C within 24 hours. The conductivity was reduced for H^+ activity according to Sjörs (1952). The concentrations of NH_4^+-N, NO_3^--N, NO_2^--N, Cl^-, SO_4^{2-} and soluble reactive phosphorus (SRP) were determined in samples filtered through Whatman GF/C filters using a Tecator flow injection analyzer. The gas diffusion method was used to estimate NH_4^+-N (Karlberg & Twengström 1983). The reaction of nitrite with sulfanilamide and N-(1-naphtyl)-ethylenediamine was used to determine NO_2^--N. NO_3^--N was determined as nitrite after reduction of the sample on the Cd-Cu column. The standard phosphomolybdenum complex method was used for SRP determination. The total N (TN) and total P (TP) values were determined as NO_3^--N and SRP respectively, after mineralization of samples using persulphate (Grasshoff et al. 1983). Cations (Ca^{2+}, Mg^{2+}, K^+, Al^{3+} and Fe^{3+}) were analyzed using an atomic absorption spectrophotometer Sectr AA640 (Varian Techtron, Australia) at the Chemistry Department of the Agricultural Faculty of the University of South Bohemia, České Budějovice.

Atmospheric deposition data was taken from the Lužnice station, ca. 20 km N of the Žofinka peatbog, which was reported annually in Anonymous (1999–2003). Element concentrations represented bulk deposition (wet plus dry deposition).

Table 1. Sources of relevés used in this study. [a] – only eight plots were sampled in 2002, because two were destroyed by other experiments. [b] – relevé made by S. Kučera.

Type of disturbance	Number of samples	Sampling year	Sample area (m^2)	Reference
burned in 2000	10	2001, 2002	25	JAKŠIČOVÁ (2003)
burned in 1994 [a]	10	2001, 2002	25	JAKŠIČOVÁ (2003)
undisturbed	5	2002	25	JAKŠIČOVÁ (2003)
windthrow-bark beetle in 1984	5	2002	25	JAKŠIČOVÁ (2003)
windthrow-bark beetle in 1984	5	1998	400	KUČEROVÁ et al. (2000)
burned in 1994	1	1998	400	KUČEROVÁ et al. (2000)
undisturbed [b]	4	1971	500	KUČEROVÁ et al. (2000)

Statistical analysis

Constrained ordination technique Redundancy Analysis (RDA) was used to analyze the vegetation composition relative to the time passed since the fire (36 relevés in total). Age since the fire (in years) was used as an environmental factor. Statistical significance of the age since the fire was tested using the Monte-Carlo permutation test (split-plot design for correction of repeatedly sampled plots). Only repeatedly sampled plots were used in this analysis (one 4-year-old and two 7-year-old burned plots that were destroyed in 2002 were excluded). Unconstrained ordination technique Principal Components Analysis (PCA) was used to analyze the vegetation composition of burned, windthrow–bark beetle and undisturbed sites (58 relevés in total). All relevés including ten older ones with different area (Table 1) were used in this analysis. Isolines of the Shannon-Weaver diversity index (Shannon & Weaver 1949) were projected onto the resulting graph. The Canoco for Windows 4.5 package (ter Braak & Šmilauer 2002) was used for all multivariate vegetation analyses.

Effects of disturbance type, sampling time and their interaction with water chemistry were tested using repeated measures ANOVA (Statistica 6 package; Statsoft 2003) followed by the post-hoc comparison, Tukey´s test. Prior to the analysis, data were log-transformed ($\log_{10}[x+1]$) because of unequal group variance and to improve normality. Correlation analysis (Pearson r correlation coefficient) was applied to log-transformed data (except pH) to unravel patterns of variation in water chemistry. For the correlation analysis the data from the burned site and those unaffected by fire were treated separately.

Results

Soil water chemistry of the undisturbed Pinus rotundata bog forest

The soil water was very acidic (mean pH = 3.42) with the lowest corrected conductivity (**Table 2**). The concentrations of all forms of inorganic nitrogen were low (inorganic N = 1.17 mg l^{-1}). Ammonium nitrogen predominated over the nitrate nitrogen. The concentrations of inorganic P (mean 0.08 mg l^{-1}) were half of the concentrations of TP. The ratio TN:TP was 23:1 indicating slight P deficiency in soil water (TN:TP > 16, Aerts et al. 1999). The Ca^{2+} concentrations ranged between 0.9-2.8 mg l^{-1} in 2003 (Fig. 2d). Cation sum (Ca^{2+} + Mg^{2+} + K^+ + Na^+ + H^+) was 459 μeq l^{-1}. The *P. rotundata* bog forest had the highest proportion of H^+ and the lowest proportion of Ca^{2+} and Mg^{2+} of the total cations (Table 3). The concentrations of H^+, NH_4^+, and Cl^- were elevated in soil water in comparison to rainwater (Table 3). The most pronounced difference was in H^+ concentrations (26.8× higher in soil water in the *P. rotundata* bog forest than in rainwater). Similarly, the mean Cl^- concentration in soil water distinctly exceeded the mean Cl^- concentration in rainwater (Table 3).

The concentration of the possibly toxic ion Al^{3+} was quite high in comparison with the base cation concentration.

Soil water chemistry of the windthrow–bark beetle affected site

The soil pH was slightly higher, but still very acidic (mean pH = 3.84) with low corrected conductivity (Table 2). No significant differences in forms of nitrogen and phosphorus were found between the undisturbed *P. rotundata* bog forest and the windthrow–bark beetle affected site. Cation sum (302 μeq l^{-1}) was lower than in the *P. rotundata* bog forest (Table 3). Considering the proportions of cations, K^+, Na^+ and Mg^{2+} were of a fairly equal importance. The concentrations of both Ca^{2+} and Mg^{2+} were low and similar to those measured at the undisturbed *P. rotundata* bog forest. The concentrations of Cl^-, Na^+, K^+ and Al^{3+} were significantly lower than at the previous site (Table 2).

Table 2. Comparison of water chemistry (means and standard deviations in parentheses) of the undisturbed *P. rotundata* forest, windthrow-bark beetle affected site and burned site on the Žofinka peatbog during 2002–2003.
n = 27 for each site. The highest concentrations of all chemical variables were measured at the burned site. Means followed by the same letter within a row are not significantly different at P = 0.05 based on ANOVA and Tukey's HSD tests. Significantly different means are in bold. Electrical conductivity (ECcorr) is expressed as μS cm^{-1}, and element concentrations as mg l^{-1}.

	Undisturbed *P. rotundata* forest	**Windthrow–bark beetle site**	**Site burned in 2000**
ECcorr	2[a] (42)	13[a] (19)	**59**[b] (65)
pH	**3.42**[a] (0.20)	3.84[b] (0.26)	4.00[b] (0.81)
NH_4^+-N	0.93[a] (0.64)	0.76[a] (0.54)	**8.08**[b] (10.31)
NO_2^--N	0.05[a] (0.03)	0.04[a] (0.02)	**0.12**[b] (0.09)
NO_3^--N	0.19[a] (0.22)	0.08[a] (0.08)	**0.74**[b] (1.73)
Total N	3.74[a] (1.12)	3.44[a] (1.19)	**15.03**[b] (12.52)
Cl^-	**9.11**[a] (4.41)	**5.63**[b] (2.80)	**11.48**[c] (3.88)
SRP	0.08[a] (0.06)	0.11[a] (0.07)	**1.38**[b] (0.94)
Total P	0.16[a] (0.05)	0.18[a] (0.07)	**1.35**[b] (1.09)
Na^+	0.75[a] (0.40)	**0.48**[b] (0.27)	0.84[a] (0.29)
Mg^{2+}	0.42[a] (0.12)	0.41[a] (0.19)	**0.85**[b] (0.35)
Ca^{2+}	2.70[a] (2.60)	3.98[a] (4.38)	**4.93**[b] (4.38)
K^+	**0.92**[a] (0.41)	**0.51**[b] (0.18)	**2.44**[c] (0.82)
Fe^{n+}	1.84[a] (0.74)	1.71[a] (1.21)	2.44[a] (1.38)
Al^{3+}	0.96[a] (0.48)	**0.61**[b] (0.47)	1.08[a] (0.58)

Soil water chemistry of the burned site

The soil water was still very acidic (mean pH = 4.00) with medium corrected conductivity (Table 2). The concentrations of NH_4^+-N, SRP (soluble reactive phosphorus) and TP were by one order of magnitude higher at the burned site than those at stands unaffected by fire (Table 2). The concentrations of NO_2^--N, NO_3^--N, and TN were several times (2.5×, 4× and 4×, respectively) higher (Table 2). Similar to the stands unaffected by fire, ammonium nitrogen predominated over the nitrate nitrogen. Extremely high concentrations of SRP (max. 4.03 mg l^{-1}) and total phosphorus (max. 4.31 mg l^{-1}) were found in the soil water especially three years after the fire (see Fig. 2b). The concentrations of SRP and TP were rather similar indicating that most of P was in dissolved inorganic form in the soil water.

We also found similarly high concentrations of SRP and total P in both newly (burned in 2000, SRP 0.42 mg l^{-1}) and old burned sites (burned in 1994, SRP 0.37 mg l^{-1}) during test measurements of soil water quality in 2001 (Fig. 2b).

The concentrations of metallic cations (K^+, Mg^{2+} and Ca^{2+}) were significantly higher at the burned site than those at stands unaffected by fire, however, they reached only several mg l^{-1}. The proportion of bases was quite similar to the previous two stands, while NH_4^+-N represented a considerably higher proportion of cations (Table 3). No significant differences in concentrations of Fe^{n+} were found throughout all three sites.

Table 3. Comparison of the ionic composition of rain and soil water (means and standard deviations in parentheses) on the Žofinka peatbog in equivalent charges of ions (μeq l^{-1}).
n = 5 for rain water (1999-2003) and N = 15 for soil water for each site in 2003. The highest concentrations of almost all chemical variables were measured at the burned site. Means followed by the same letter within a row are not significantly different at P = 0.05 based on ANOVA and Tukey's HSD tests (only directly comparable values between study sites were tested). Significantly different means are in bold. The cation sum was calculated as sum of H^+, Na^+, Mg^{2+}, Ca^{2+} and K^+. Rainwater data were annually measured means taken from bulk collectors in the Lužnice station, ca. 20 km N of the Žofinka peatbog.

	Rainwater	**Undisturbed *P. rotundata* forest**	**Windthrow–bark beetle site**	**Site burned in 2000**
Cation sum	111 (69)	459^{a} (122)	**302**^{b} (106)	463^{a} (179)
H^+	12 (5)	322^{a} (114)	176^{ab} (89)	129^{b} (93)
Na^+	14 (6)	**21**^{a} (4)	**14**^{b} (4)	**34**^{c} (6)
Mg^{2+}	13 (10)	31^{a} (10)	37^{a} (19)	**81**^{b} (31)
Ca^{2+}	53 (38)	60^{a} (19)	61^{a} (24)	**145**^{b} (117)
K^+	19 (14)	**25**^{a} (10)	**14**^{b} (3)	**74**^{c} (17)
NH_4^+	39 (20)	84^{a} (50)	64^{a} (48)	**965**^{b} (794)
Cl^-	32 (30)	**208**^{a} (117)	**116**^{b} (39)	**315**^{c} (96)

Annual and seasonal variability in water chemistry

Statistically significant increases of mean concentrations of NH_4^+-N ($F = 71.05$, $P << 0.001$), NO_2-N ($F = 6.28$, $P = 0.02$), total P ($F = 9.43$, $P = 0.006$), total N ($F = 27.91$, $P << 0.001$), K^+ ($F = 11.67$, $P = 0.003$), Mg^{2+} ($F = 7.88$, $P = 0.01$), Fe^{n+} ($F = 20.00$, $P = 0.0002$) and Al^{3+} ($F = 14.28$, $P = 0.001$) were found at the burned site between 2002 and 2003 (repeated measures ANOVA, post-hoc comparison Tukey test). For example, the mean concentration was twofold higher for TP, almost 4 times as high for TN and 10 times as high for NH_4^+-N in 2003 than in 2002 at the burned site. Additionally, according to measurements of water quality done in 2001, the concentrations of SRP, total P and total N showed a steady increase between 2001 and 2003 at the burned site (Fig. 2a, b). At the same time, the mean concentrations of the above-mentioned nutrients were similar at both the *P. rotundata* bog forest and windthrow–bark beetle affected site, except for the Fe^{n+} increase at the windthrow–bark beetle affected site in 2003.

There was a marked decline, however, in concentrations of Ca^{2+} and Na^+ throughout all sites from 2002 to 2003. Concentrations of Ca^{2+} steadily decreased during the 2002 growing period, being the highest at the burned site and windthrow–bark beetle affected site (Fig. 2c, d).

At both the *P. rotundata* bog forest and the windthrow–bark beetle affected site, the concentrations of SRP, NH_4^+-N, TP, and pH were negatively correlated with the groundwater table (Table 4). Corrected conductivity did not correlate with pH while it correlated positively with NH_4^+-N, SRP, NO_2^--N, Cl^-, TN and Fe^{n+}. At the burned site, only Fe^{n+} concentrations correlated significantly with the groundwater table (Table 4). Both corrected conductivity and pH correlated positively with the concentrations of NH_4^+-N, SRP, TP and TN.

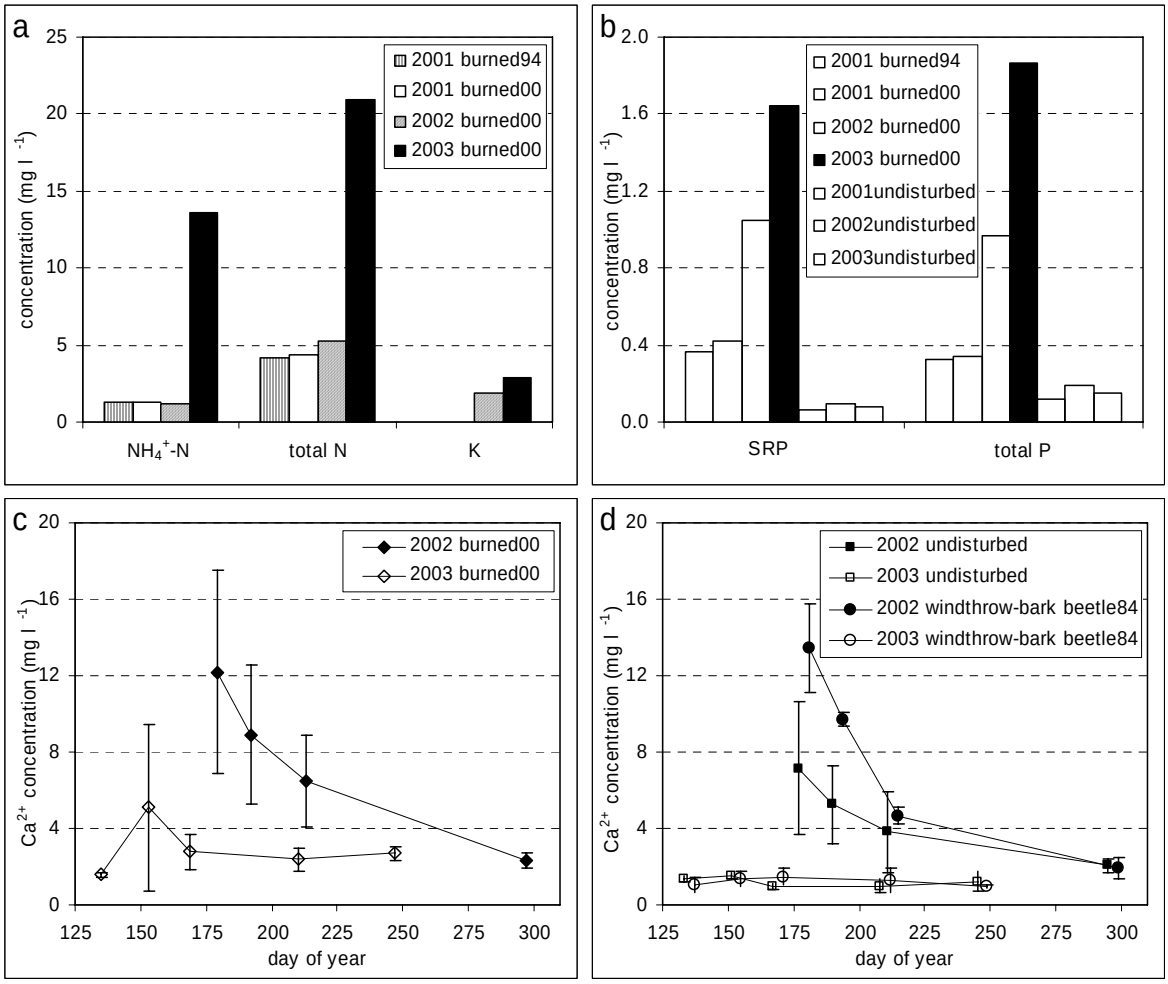

Fig. 2. (a) Increasing concentrations of NH_4^+-N, total N and K^+ at the site burned in 1994 (burned94) and 2000 (burned00) during three growing seasons (2001–2003). (b) Increase of soluble reactive phosphorus (SRP) and total P concentrations in soil water at the burned sites compared with soil water concentrations in the *Pinus rotundata* forest (undisturbed) during three growing seasons (2001-2003). In some cases concentrations of total P were ca 10% lower than the concentrations of SRP, which is in the range of analytical error. (c) Steadily decreasing Ca^{2+} concentrations at the site burned in 2000. (d) Decreasing Ca^{2+} concentrations in the *P. rotundata* forest and at the windthrow-bark beetle affected site (windthrow-bark beetle84) during the 2002 growing season, compared to the stable low Ca^{2+} concentrations in 2003. Points for the windthrow sites are slightly shifted (+3 days) on x-axis to reduce overlapping with undisturbed sites. The first four digits in the legend mean the year of soil water sampling.

Post-fire vegetation succession

Three categories of species could be distinguished from the burned sites (RDA analysis, Fig. 3): (i) initial colonizers – the species whose cover negatively correlated with the environmental factor "age = time after the fire" (left half of the RDA plot). The most common were anemochorous species (weedy species e.g. *Taraxacum* sp. div., *Epilobium* sp. div., *Conyza canadensis, Senecio* sp. div.), seedlings of *Populus tremula* and *Salix* sp. div., and the bryophytes typical for disturbed sites, e.g. *Marchantia polymorpha, Ceratodon purpureus, Pohlia nutans* and *Funaria hygrometrica*. Further, species typical for the *P. rotundata* bog forest – *Avenella flexuosa* and juveniles of *Frangula alnus* were among the first colonizers; (ii) the species whose cover positively correlated with "age = time after the fire". These are characteristic species of the wooded peatbogs, e.g. ericaceous dwarf shrubs (*Vaccinium myrtillus, V. vitis-idaea, Ledum palustre, Calluna vulgaris*), *Betula* sp. div., *Picea abies* and

Table 4. Correlation coefficients between chemical variables and groundwater table (GWT) for the undisturbed *P. rotundata* forest and windthrow–bark beetle affected site (part under diagonal), and for the burned site (part above diagonal), respectively. Log-transformation ($log_{10}[x+1]$) was applied to all variables except pH. Correlations marked bold are significant ($P < 0.05$). n = 27 for each variable. Grey cells indicate pairs of significant-insignificant (or vice versa) correlation coefficients between the undisturbed plus windthrow–bark beetle affected site and the burned site, respectively.

	ECcorr	pH	NH_4^+-N	SRP	NO_2^--N	NO_3^--N	Cl^-	Total N	Total P	Na^+	Mg^{2+}	Ca^{2+}	K^+	Fe^{n+}	Al^{3+}	GWT
Eccorr		**0.91**	**0.63**	**0.89**	0.45	0.05	0.34	**0.83**	**0.84**	0.19	-0.10	-0.04	0.29	0.29	0.22	-0.17
pH	0.09		**0.60**	**0.91**	**0.67**	-0.21	0.50	**0.75**	**0.90**	-0.01	-0.35	-0.21	0.15	0.35	0.27	-0.09
NH_4^+-N	**0.64**	**0.38**		0.51	0.42	-0.28	**0.54**	0.40	0.45	0.16	-0.11	-0.03	0.21	0.47	0.24	-0.11
SRP	**0.48**	**0.51**	**0.81**		**0.65**	-0.08	0.46	**0.84**	**0.95**	-0.10	-0.31	-0.18	0.06	0.31	0.29	-0.16
NO_2^--N	**0.36**	**-0.69**	0.09	0.09		-0.45	**0.65**	**0.59**	**0.70**	-0.17	**-0.53**	-0.34	0.25	0.30	0.34	0.16
NO_3^--N	-0.03	-0.30	0.15	-0.21	-0.04		**-0.84**	0.05	-0.15	0.38	**0.77**	0.14	0.34	-0.51	**-0.52**	-0.10
Cl^-	**0.59**	**-0.66**	0.17	0.08	**0.87**	0.02		0.35	0.50	-0.24	**-0.61**	-0.13	-0.17	**0.63**	**0.70**	-0.08
Total N	**0.57**	-0.27	**0.71**	**0.55**	**0.59**	0.30	**0.63**		**0.91**	0.13	-0.27	-0.07	0.36	0.04	0.21	0.16
Total P	0.27	**0.36**	**0.63**	**0.82**	0.03	-0.08	0.03	**0.55**		-0.05	-0.44	-0.26	0.12	0.20	0.29	0.04
Na^+	0.33	**-0.68**	0.19	0.03	**0.82**	0.13	**0.82**	**0.65**	0.07		0.40	0.16	**0.80**	-0.19	-0.34	-0.06
Mg^{2+}	0.34	0.05	**0.37**	**0.49**	**0.45**	-0.25	**0.37**	**0.50**	0.42	**0.49**		0.26	0.27	-0.23	-0.23	-0.34
Ca^{2+}	0.32	-0.23	0.26	0.31	**0.61**	-0.24	**0.58**	**0.48**	0.19	**0.70**	**0.79**		0.01	-0.12	0.24	-0.06
K^+	0.35	0.01	**0.60**	0.20	-0.03	**0.45**	0.11	**0.44**	0.27	0.30	-0.15	-0.06		-0.15	-0.34	0.13
Fe^{n+}	**0.37**	-0.11	0.32	**0.40**	**0.61**	-0.25	**0.53**	**0.55**	0.30	**0.60**	**0.92**	**0.82**	-0.20		0.39	**-0.70**
Al^{3+}	0.26	**-0.52**	-0.03	-0.04	**0.59**	-0.18	**0.58**	**0.39**	-0.08	**0.49**	0.16	**0.41**	-0.13	**0.37**		-0.15
GWT	-0.36	**-0.66**	**-0.66**	**-0.64**	0.28	0.29	0.23	-0.21	**-0.43**	0.21	-0.26	-0.08	-0.21	-0.21	0.05	

bryophytes *Pleurozium schreberi, Dicranum polysetum* and *Sphagnum capillifolium*; (iii) the species whose cover did not correlate with "age = time after the fire", e.g. *Dryopteris carthusiana, Andromeda polifolia, Vaccinium uliginosum, Polytrichum* sp. and *Sphagnum magellanicum*.

The moss layer especially regenerated in the wet depressions. Ericoid shrubs regenerated quickly, mostly by resprouting from underground fragments but only seedlings of *Calluna vulgaris* were found more frequently. Seedlings of both Scots pine (*Pinus sylvestris*) and birch (*Betula* sp. div.) often occurred, however, the edificator of the former community – *P. rotundata* – was mostly absent.

Vegetation of disturbed sites

Vegetation relevés from differently affected stands (burned, windthrow–bark beetle and undisturbed, respectively) were analyzed using the PCA ordination with only species of the moss and herb layers included (both species from shrub and tree layers excluded, Fig. 4a, b). The stands were clearly distinguished according to the type of disturbance. The most similar sample plots were those from the first and second and those from the seventh and eighth year after the fire (Fig. 4b). The sample plot from the fourth year after the fire was closer to sample plots from the seventh and eighth year after the fire. Sample plots from the windthrow–bark beetle affected sites were most similar to the undisturbed *P. rotundata* bog forest. Few sample plots differing in their area did not affect this pattern and appeared mixed or close to the plots with the same type of disturbance.

Anemochorous species, indicating stands shortly after the fire (left half on the species plot, Fig. 4a) usually disappeared within two or three years. During the post-fire succession especially *Molinia caerulea* and saplings of *Betula* sp. started to dominate in the understorey (upper part on the species plot, Fig. 4a).

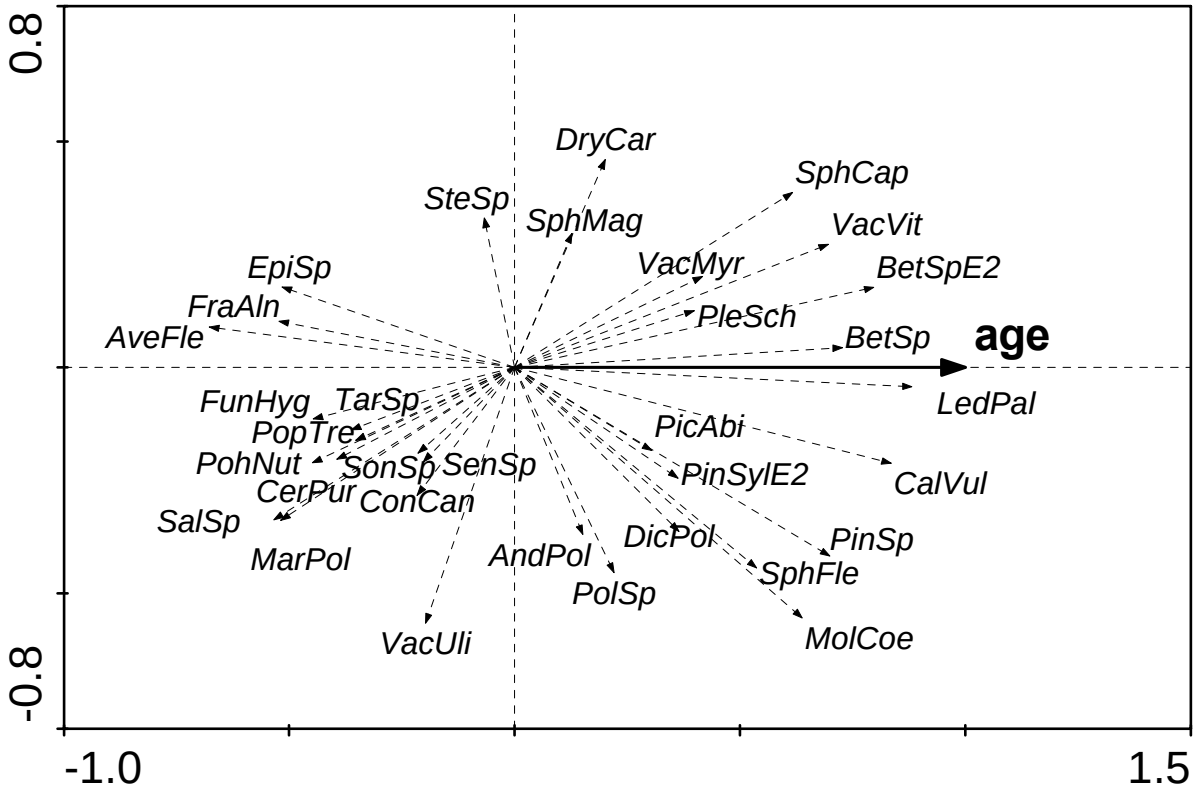

Fig. 3. Post-fire succession in the Žofinka peatbog with shrub and tree layers included in the analysis (species plot of the RDA analysis, sample plots from the sites burned in 1994 and 2000, respectively). Age of the burned site was used as an environmental factor. The first RDA axis explained 31% of the variability in the species data. The effect of age of the burned site was highly significant (Monte Carlo permutation test, N = 999, $P = 0.001$; F-ratio =15.25).
AndPol (*Andromeda polifolia*), *AveFle* (*Avenella flexuosa*), *BetSp* (*Betula* sp.), *BetSpE2* (*Betula* sp. E2), *CalVul* (*Calluna vulgaris*), *CerPur* (*Ceratodon purpureus*), *ConCan* (*Conyza canadensis*), *DicPol* (*Dicranum polysetum*), *DryCar* (*Dryopteris carthusiana*), *EpiSp* (*Epilobium* sp.), *FraAln* (*Frangula alnus*), *FunHyg* (*Funaria hygrometrica*), *HylSpl* (*Hylocomium splendens*), *LedPal* (*Ledum palustre*), *LeuGla* (*Leucobryum glaucum*), *MarPol* (*Marchantia polymorpha*), *MolCoe* (*Molinia caerulea*), *OxyPal (Oxycoccus palustris), PicAbi* (*Picea abies*), *PinSp* (*Pinus* sp.), *PinSylE2* (*Pinus sylvestris* E2), *PleSch* (*Pleurozium schreberi*), *PohNut* (*Pohlia nutans*), *PolSp* (*Polytrichum* sp.), *PopTre* (*Populus tremula*), *SalSp* (*Salix* sp.), *SenSp* (*Senecio* sp.), *SonSp* (*Sonchus* sp.), *SphCap* (*Sphagnum capillifolium*), *SphFle* (*Sphagnum flexuosum*), *SphMag* (*Sphagnum magelanicum*), *SteSp* (*Stellaria* sp.), *TarSp* (*Taraxacum* sp.), *VacMyr* (*Vaccinium myrtillus*), *VacUli* (*Vaccinium uliginosum*), *VacVit* (*Vaccinium vitis-idaea*)

A luxuriant herb layer of ericoid dwarf shrubs (*Ledum palustre, Vaccinium myrtillus, V. vitis-idaea,* and *V. uliginosum*), low scattered trees (up to 8 m), dead trees and snags were the characteristic feature of the stands disturbed by wind or by both wind and insect infestation. *Sphagnum flexuosum* or *S. fallax* and some dwarf shrubs (*Oxycoccus palustris*) occurred in wet depressions created by uprooted trees (right half on the species plot, Fig. 4a). Compared to the undisturbed *P. rotundata* forest, *Frangula alnus, Betula pendula,* and *Pinus sylvestris* occurred often in the lower tree layer. Therefore, sample plots from the windthrow–bark beetle affected sites were mixed-up with sample plots from the undisturbed *P. rotundata* bog forest only when both species from shrub and tree layers were excluded from the ordination (Fig. 4b).

Understorey plant communities of undisturbed *P. rotundata* forest and that developed after fire and windthrow followed by bark beetle attack shared all herb species and ca. 65% of moss species, even if the total cover of herb and tree layer was quite different. *Frangula alnus* occurred in highest abundances in windthrow–bark beetle affected sites (1% mean coverage in 18-year-old plots) followed by old burned plots (mean coverage 0.4% in 7- and 8-year-old plots) and was absent in undisturbed plots. Fire promoted a rapid expansion of *Molinia caerulea* (mean coverage 27% in 7- and 8-year-old burned plots in comparison with 4.7% in the 18-year-old windthrow–bark beetle affected plots). *Molinia caerulea* had very low coverage in undisturbed plots (mean coverage 0.1% in relevés from 2002).

The lowest species diversity indicated by Shannon's index (Fig. 4b) was found for 1-year-old burned plots. After that there is a growth of diversity towards wind-damaged and undisturbed *P. rotundata* forest.

Discussion

Vegetation of windthrow–bark beetle affected and undisturbed sites

Unlike fires, both windthrow and bark beetle outbreak directly affected only canopy trees. Therefore, the species composition at windthrow–bark beetle affected sites and at undisturbed *P. rotundata* bog forest differed mainly in shrub and tree layers. A new tree layer was established especially by young individuals of *P. rotundata* (partly also by *P. sylvestris*), which were already present as saplings in the stands prior to the disturbance (Kučerová, unpubl. data). Similarly, Fischer et al. (2002) documented a successful regeneration of the spruce tree layer from the young spruce saplings already present on plots destructed by windstorm in the Bavarian National Park.

However, *P. sylvestris* saplings became more abundant than *P. rotundata* saplings at the windthrow–bark beetle affected sites. Higher admixture of *P. sylvestris* in the new tree layer would increase the possibility of the next introgressive hybridization of the *P. rotundata* population with *P. sylvestris* on the locality – the process already documented for several *P. rotundata* populations in the Třeboň Basin (Businský 1998, Rektoris et al. 2003). Therefore, further long-term prosperity of the *P. rotundata* population seems quite uncertain in the Žofinka peatbog.

Almost all species of both herb and moss layer successfully survived (or recolonized the site) 18 years after canopy break-up. Nevertheless, some species (especially *Frangula alnus* and *Molinia caerulea*) occurred in higher abundances at the windthrow–bark beetle affected sites. Both species could be positively affected by disturbance event (soil disturbance, higher light levels) or by higher nutrient concentrations. However, no differences were found in N and P soil water concentrations at the undisturbed *P. rotundata* bog forest and at the windthrow–bark beetle affected site. Release of nutrients from fallen trees has been rather slow in contrast to fire. Released nutrients were probably incorporated into the already present ericoid shrubs and mosses, allowing them to expand their coverage. Both species (*Frangula alnus* and *Molinia caerulea*) probably expanded from the already present individuals to the places with low herb and moss coverage in between former trees being supported by higher light levels. As the stands were not cleared after the windstorm the soil disturbance was restricted to the pit-and-mound system created by uprooted trees. Such places were colonized by several pioneer species (*Rubus idaeus*, *Betula* sp., etc.) in mountain spruce forests in the Bavarian Forest National Park (Fischer et al. 2002). In our case the pits were primarily suitable for the colonization of *Sphagnum* sp. due to the high groundwater table while dry-tolerant mosses and lichens especially colonized mounds.

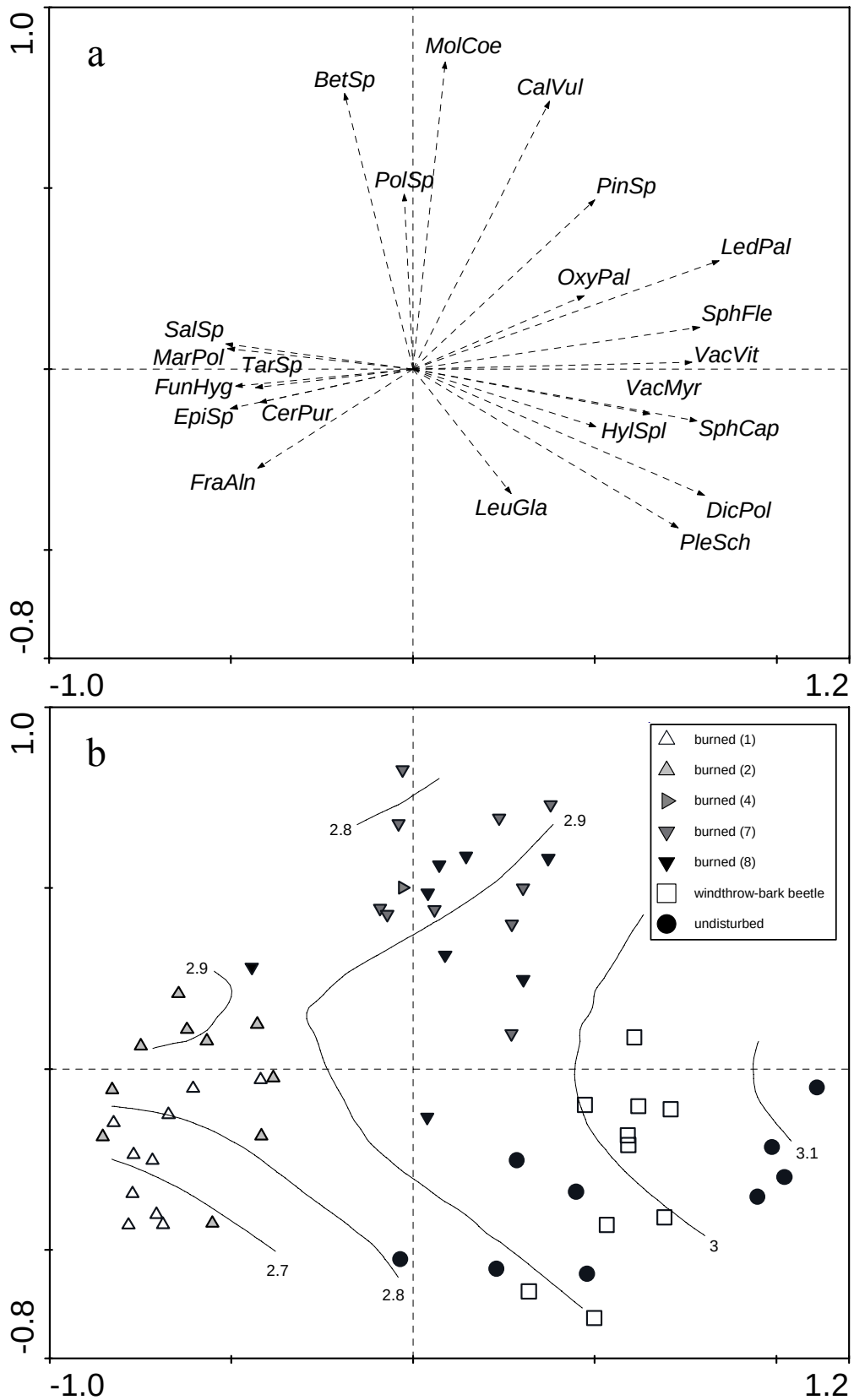

Fig. 4. Increasing species diversity from differently affected to undisturbed plots in the Žofinka peatbog with shrub and tree layers excluded from the analysis. Species (a) and samples (b) plot of the PCA analyses are depicted, with samples from burned (number in brackets indicates time since burning in years), windthrow–bark beetle affected and undisturbed *P. rotundata* sites. Isolines correspond to Shannon-Weaver index of species diversity. The first and second PCA axes explained 30.7% and 15.0% of the variability in the species data, respectively. For explanation of species abbreviations see Fig. 3.

Post-fire vegetation succession

Holubičková (1960) reported surface peat fires from the Mrtvý luh peatbog (Upper Vltava river valley) in the 20th century. The post-fire vegetation was similar to that in undisturbed stands, only trees and some sensitive species were absent (e.g. *Andromeda polifolia* and *Oxycoccus palustris*). This record corresponded with our findings. Jankovská (1980), however, found evidence of the effect of periodic fires on the *P. rotundata*-dominated peatbogs in the Třeboň Basin during the Subatlantic period (charcoal layers in peat sediments in Červené blato bog, 10 km from the study site, and Borkovická blata bog). Those probably deep ground fires temporarily increased the cover of the *Rhynchosporion albae* Koch 1926 communities, especially of *Scheuchzeria palustris*. The former *P. rotundata*-dominated communities regenerated during the time.

In some aspects, the post-fire succession in the *P. rotundata* bog forest seems to resemble the post-clearing succession in mountain spruce forests (Fischer et al. 2002, Jonášová & Prach 2004). Fire created large-scale open habitats very suitable for invading species similar to that usually made during forest clearing. During succession weeds quickly disappeared and the grasses (*Calamagrostis villosa* in spruce forest, Fischer et al. 2002, compared to *Molinia caerulea* in the *P. rotundata* bog forest) started to dominate in the herb layer. Both vascular plants and mosses characteristic of the *P. rotundata* bog forest steadily increased their abundance during the post-fire succession. However, the abundance of light- and nutrient-demanding species increased markedly in comparison to the former *P. rotundata* bog forest. Additionally, the edificator of the former community – *P. rotundata* – decreased considerably in favour of *P. sylvestris* and *Betula* sp. div.

Soil water was still very acidic and deficient in cations even after total mineralization of surface organic matter by burning and subsequent increase of nutrient concentrations for plant growth (especially N and P, see Table 2). This corresponded with the post-fire vegetation succession. During a very short period (2-3 years) the present species were mostly the same as those at the unaffected stands, i.e., acidophilous species tolerating low cation saturation.

Almost all dissolved phosphorus in the soil water was present in inorganic form indicating low microbial activity. The excess of N and P in soil water could result from a relatively low uptake of these nutrients by sparse vegetation in the beginning of the post-fire succession. Additionally, the species present probably could not use all available nutrients because of their slow growth, high nutrient reutilization or a relative unavailability of these nutrients due to low pH as speculated for bog plants by several authors (Waughman 1980, Aerts et al. 1999).

However, high concentrations of both inorganic N and P available in both soil surface and soil water along with the effect of disturbance probably had a positive effect on the growth of some plants (e.g. vigorous growth of *Molinia caerulea* and *Betula* sp.). Loach (1968) documented very large growth increases of *Molinia caerulea* after P additions in combination with other elements (N, K). *Molinia caerulea* is even tolerant of burning (Taylor et al. 2001), so it could very rapidly colonize the burned sites. Similarly, growth of *Betula pendula* was positively affected by N additions with simultaneous high P loads (Tomassen et al. 2003).

High concentrations of inorganic P at the burned soil surface could promote colonization of *Sphagnum* from spores together with many other bryophytes (e.g. *Pohlia nutans, Polytrichum strictum*) as reported by Rydin (1986) and Sundberg & Rydin (2002). Actually, we reported successful colonization of wet depressions by several *Sphagnum* species (e.g., *S. capillifolium, S. flexuosum,* and *S. fallax*) at the site burned in 1994. The site burned in 2000 was colonized by several bryophytes typical for the *P. rotundata* bog forest (*Polytrichum* sp. div., *Aulacomnium palustre*) during one year.

Soil water chemistry of the P. rotundata bog forest

Two interesting results in soil water chemistry of the *Pinus rotundata* bog forest were found during the study.

(i) Very low pH, in comparison with the studies made in similar vegetation (cf. Neuhäusl 1975, Bufková et al. 2005), the lowest pH values were measured directly in the *P. rotundata* bog forest in the Žofinka peat bog;

(ii) Rather high concentration of SRP (soluble reactive phosphorus) even in the undisturbed *P. rotundata* bog forest (cf. Gorham et al. 1984, Tahvanainen et al. 2002, Bragazza et al. 2003). Similar high concentrations of both H^+ and SRP were measured simultaneously in the *P. rotundata* bog forest in the Červené blato peatbog (Kučerová, unpubl. data), 10 km from the Žofinka peat bog;

Because the area receives little pollution (cf. Anonymous 1999-2003, Pokorný & Kučerová 2000), there are two possible explanations. First, the Žofinka peatbog is situated in the lowest altitude in the *Pino rotundatae-Sphagnetum* range with rather low precipitation and rather high air temperature during the vegetation period. According to Gorham et al. (1984) very low pH values in soil water are typical for such continental bogs. The mineralization could proceed here faster than in mountain peatbogs because of the higher temperature and higher groundwater fluctuation. Additionally, the soil profile was not so intensively washed by rainwater. Therefore, the mineralization products (especially H^+, coloured humid acids, but also SRP, NH_4^+-N) could accumulate in the soil water while most cations were incorporated in the biomass. This corresponded with the negative correlation of the concentrations of NH_4^+-N, SRP and total P to groundwater table (see Table 4) in both *P. rotundata* bog forest and windthrow–bark beetle affected site. Similarly, Wilson & Fitter (1984) documented fast P mineralization under conditions of low pH and low groundwater table. High values of available P in soil solution could be ensured by high turnover rates even though P inputs may be low (Kellogg & Bridgham 2003). Nevertheless, P availability for plants could be reduced by changes in Fe and Al dynamics in soil water through complexation of dissolved phosphate (Darke & Walbridge 2000, Pant & Reddy 2001).

Second, high acidity, elevated concentrations of dissolved P and simultaneously low availability of cations could be a consequence of the long-term influence of previous drainage (in the beginning of the 20th century). Similarly, von Sengbusch et Bogenrieder (2001) found acidification of the upper peat horizon along with the lower groundwater levels and the decreased availability of both calcium and magnesium in previously drained *P. rotundata* forests in the southern Schwarzwald Mts., Germany.

Small-scale dust pollution from the burned site could be a reason for the relatively high soil water concentrations of Ca^{2+} throughout all sites in June 2002 (i.e., 10 months after the fire, Fig. 2c, d). The pronounced decrease of Ca^{2+} concentrations during 2002, and almost equal concentrations in 2003 could correspond to a rapid uptake of Ca^{2+} by vegetation or to its adsorption to soil particles. The mean Ca^{2+} concentrations in 2003 were close to the values given for mountain peatbogs (mean 0.9 mg l^{-1} in *Pinus mugo-Sphagnum capillifolium* community, Rybníček 2000). Al concentrations, however, were quite high in comparison with the base cation concentrations. In the Žofinka peatbog, the molar ratio of $Ca:Al_{total}$ was never lower than 0.3, which is considered as 'critical thresholds' below which damage to temperate tree species is frequent (Cronan & Grigal 1995).

Several authors (e.g. Clymo 1983, Tallis 1983) reported extremely high peak concentrations of both P and K after fire. Contradictory to these studies, we did not find extremely high peak concentrations of K^+. We measured a gradual increase in concentrations of all dissolved forms of N and P after fire (see Fig. 2a, b) probably resulting from a dissolution and redistribution of released N and P from the soil surface towards soil water.

Additionally, P adsorption in the peat soil could be saturated three years after the fire, resulting in higher P concentration in soil water (Richardson 1985).

The similarly high concentrations of SRP and total P in both newly and old burned sites could indicate the long-term persistence of higher phosphorus levels in the soil water at the old burned site. However, according to terrain slope (Koroš et al. 1998), small distance and relatively high mean saturated hydraulic conductivity (0.176 m day^{-1}, Kučerová, unpubl. data), there was a possibility of subsurface flow of soil water in the direction from the newly burned site towards the old one associated with nutrient flux (see Fig. 1).

Conclusion

Only low differences were found in the soil water chemistry between windthrow-bark beetle affected and undisturbed *P. rotundata* forest sites. The species composition of the moss and herb layer after 18 years of natural succession was similar to the vegetation without wind damage. However, the documented long-term changes of the tree and shrub layer could be partly irreversible (increase in *P. sylvestris* density). Even if the natural succession after wind damage maintained most of the species diversity in the peatbog, the accumulation of highly flammable dead wood increased the probability of a fire. Occasional fires could substantially change both the species composition and the soil water chemistry. A short-term increase of weeds was followed by a decrease in species diversity and by an increase in dominance of some competitive species (*Molinia caerulea*). However, a temporary higher groundwater table after canopy break-up could positively affect regeneration of the moss layer. The species composition of the tree and herb layer changed more after the fire than after the wind damage, probably with long-term consequences. Concentrations of nutrients released by burning (especially N and P) increased markedly in soil water compared to stands affected by both windthrow and bark beetle attack.

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VEGETATION CHANGES OF PINUS ROTUNDATA BOG FOREST IN THE ŽOFINKA NATURE RESERVE, TŘEBOŇ BIOSPHERE RESERVE

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Abstract
The "Žofinka" peat-bog was recognised as the best preserved locality of the *Pinus rotundata* bog forest in the Třeboň Basin at the beginning of 1970´s. The development of the locality since the 1970´s and the description of vegetation changes there were the main objectives of the study. The unpublished material of S. Kučera was used for the evaluation of vegetation in 1970´s. During the vegetation period 1998 the vegetation mapping was performed to detect vegetation changes in the reserve in the last 20 years. The previous *Pino rotundatae-Sphagnetum* community, only marginaly influenced by man in the past, was strongly affected by natural disturbances (wind, insect infestation and partly by fire). Especially the most valuable stands of the former *Pinus rotundata* forest have been strongly affected by both windbreaks and insects. Canopy break-up resulted in expansion of ericoid dwarf shrubs. Besides the changes in radiation environment and temperature amplitudes in the understory, also changes of water table fluctuation were remarkable. Nowadays, substitutive stands, replacing the previous *Pinus rotundata* forest, are the main vegetation type on the locality. We can concluded that the regeneration of the community is succesfull on the most locality. Remaining question is how strong could excavation of peripheral channels in 1970´s affect the vegetation change described above.

Keywords: *Pinus rotundata*, peat-bog, monitoring, vegetation change, water table fluctuation, Czech Republic

Nomeclature: Species names of vascular plants and bryophytes follow Ehrendorfer (1973) and Frey et al. (1995), respectively.

Introduction

The occurrence of peat-bogs in the Třeboň Basin is enabled by suitable hydrogeological conditions of the area, especially by insufficient drainage conditions in the plain, high regional groundwater table, numerous flushes from artesian waters and by a high representation of clayey soils creating watertight layers (Jeník et Přibáň 1990). Most peat-bogs in the Třeboň Basin are topogenic formations originating in sites flooded locally by ground water which drained along stratigraphic faults to the surface (Procházková 1978). In case of high thickness of peat sediments only the deepest peat layers are saturated by nutrient rich water, while the peat surface is primarily fed with precipitation water (Rektoris et al. 1997, Kolmanová et al. 1999). Therefore, present ground vegetation on deep peatbogs is considered to be uninfluenced by nutrient rich ground water. Nowadays, a part of the deep peatbogs in the Třeboň Basin is occupied by vegetation of the (sub)continental raised bogs (treed bogs or Waldhochmoore).

The (sub)continental raised bogs exist in a state of incomplete water saturation as a result of low precipitation (e. g., 600–700 mm per year in the Třeboň Basin), long dry periods in summer and intensive evapotranspiration. Water shortage restricts the growth of *Sphagnum* species, which in turn favours establishment and growth of seedlings of trees and dwarf shrubs (Neuhäusl 1972). As a result, vigorous stands of *Pinus rotundata* are found on the bogs of the Třeboň Basin – *Pino rotundatae-Sphagnetum* community (Kästner et Flössner 1933 corr. Neuhäusl 1972). The bog forests are usually more than a hundred years old, often dense and tall and they are close to the northern taiga ecosystem (Rektoris 1994).

Pinus rotundata Link (sensu Skalická 1988) and its stands occur from submountain to mountain peat-bogs in the central Europe (for distribution maps see Meusel et al.1965, Neuhäusl 1972). Localities in the Třeboň Basin represent their lower altitudinal range. According to Businský (1998) *Pinus rotundata* Link is an independent species from the complex of *Pinus mugo* Turra. This taxonomically complicated complex of European pines is represented by the group of evolutionally young taxa that hybridize intensively each other, even fertile hybrids with *Pinus sylvestris* L. are found. The interspecific hybrid combination *P. rotundata* × *P. sylvestris* [= *P.* × *digenea* Beck.] occurs commonly at present localities of *P. rotundata* in the Třeboň Basin. As a result of introgressive hybridisation variable hybrid populations often occur there (Businský 1998).

Vegetation similar to the recent *Pinus rotundata* bog forests has occurred in peat-bogs of the Třeboň Basin since the Atlantic period (Jankovská 1980). Most of these species had already been present there as a part of the postglacial vegetation as it is assumed that migration of such heliophillous species was improbable to occur through dense mesophillous forests of the Atlantic period.

Available evidences indicate that before the bogs were affected by human activities their central parts were wetter, rather open, only with scattered stunted *Pinus rotundata* trees, in the understory *Sphagnum* species, *Eriophorum vaginatum* and dwarf shrubs dominated (Jankovská 1980). Higher tree densities were limited to the edges of the bogs. As both tree height and density are affected by the depth of water table and its fluctuations, drainage inside a peat-bog could change vegetation zonation in the past – towards denser forest growth. Also drainage of neighbouring forests could accerelate a succession shift to the denser and more advanced forest vegetation inside peat-bogs. In contrary, extensive deforestation in the surroundings could enhance peat growth and slow down decomposition owing to rise of local water table as have been found by Speranza et al. (in prep.) in the Černá hora bog, Krkonoše Mts.

Intense forest exploatation (charcoal production for glassworks, metalworks etc.) in the end of 18th century resulted in large-scale degradation of forests in the central Europe. In consequence new forest schools, forest cultivation and planting of monocultures were established besides the search for alternative fuel. First references of drainage and turf digging have been recorded since the end of 18th century in the Třeboň Basin (Spirhanzl 1951). Drainage or peat extraction affected all peatbogs found in the Třeboň Basin.

The "Žofinka" peat-bog was recognised by the botanist S. Kučera at the beginning of 1970´s as the best preserved locality of the *Pinus rotundata* bog forest in the Třeboň Basin. He made its first botanical exploration and proposed the locality for a nature reserve. Owing to this, the locality was prevented from destruction as a large-scale drainage and planting of *Pinus sylvestris* were planed there.

How the development of the locality has been proceeding since the 1970´s and the description of vegetation changes there were the main objectives of this study.

Site description

The study site (130 ha) is located in the southern part of the Třeboň Biosphere Reserve in the Czech Republic, 22 km south of Třeboň (Fig. 1a). The "Žofinka" peat-bog (48°49´N, 14°53´E, 470–475 m a.s.l.) is a continental raised bog (sensu Neuhäusl 1972) or treed bog dominated by *Pino rotundatae-Sphagnetum* (Kästner et Flössner 1933 corr. Neuhäusl 1972) community, *Oxycocco-Sphagnetea* class.

The peat-bog is situated in a shallow depression of the Cretaceous bedrock. The bedrock is made up of sediments of the Klikov series – sand, clay and clayey sand (Koroš et al. 1998). The bedrock is very acid, poor in nutrients. According to Koroš et al. (1998) the peat-bog originated from a gradual local subsidence of the Cretaceous bedrock, consequently followed by local increase of water table.

The bog surface is flat. Maximum peat depth is about 4 m. Two deep drainage channels demarcate the Reserve in the NW and NE (Fig. 1b). Both channels were dug out in the past and were excavated to the present depth of 2 m in the 1970´s. Two shallow drainage ditches (cca 0.5 m deep), penetrating the central part of the bog in NW–SE direction, discharge out at the NW channel on the Reserve´s edge. The northern part of the peatbog was strongly disturbed by turf digging in the last century and in the beginning of 20th century (Kučera 1977). These sites were not included into the Reserve. Further the NE part of the Reserve was affected by turf digging in the 1950´s, the surface was cut of about 1 m.

Mean annual temperature is above 7 °C over the Třeboň Basin (Přibáň et al. 1992) and mean temperature for vegetation period (April–September) is about 14 °C. The climate is rather continental with 600–650 mm of precipitation. Precipitation in summer is considerably higher (400–450 mm) than in winter.

Methods

Evaluation of vegetation changes

The unpublished material of S. Kučera (Kučera 1977) was used for the evaluation of vegetation in 1970´s – 16 phytosociological relevés from 1971, located on the map and the actual vegetation map from 1977 in a scale 1:10 000. Phytosociological relevés were sampled using the 5-grade Braun-Blanquet scale. During the vegetation period 1998 the vegetation mapping was performed in the same scale 1:10 000 to detect successional changes in the nature reserve in the last 20 years. 26 phytosociological relevés were sampled using a modified version of the 7-grade Braun-Blanquet scale with the grade 2 subdivided into 3 subgrades. A part of the relevés was situated near to the relevés made by Kučera (1977), a part was collected to describe new vegetation types on the locality.

In this study the conception of subcontinental raised bogs given in Neuhäusl (1972) and Rybníček et al. (1984) was followed because recent syntaxonomical study of the treed bogs is lacking. Therefore we classified the *Pinus rotundata* dominated stands as *Pino rotundatae-Sphagnetum* (Kästner et Flössner 1933 corr. Neuhäusl 1972) community, *Oxycocco-Sphagnetea* class. However, some authors (Oberdorfer 1992, Pott 1995, Schmidt et Bogenrieder 1998) included similar stands to the discrete community *Vaccinio uliginosi-Pinetum rotundatae* Oberd. 34 emend., class *Vaccinio-Piceetea* (boreo-alpin coniferous forests), because of their structure close to that of forests.

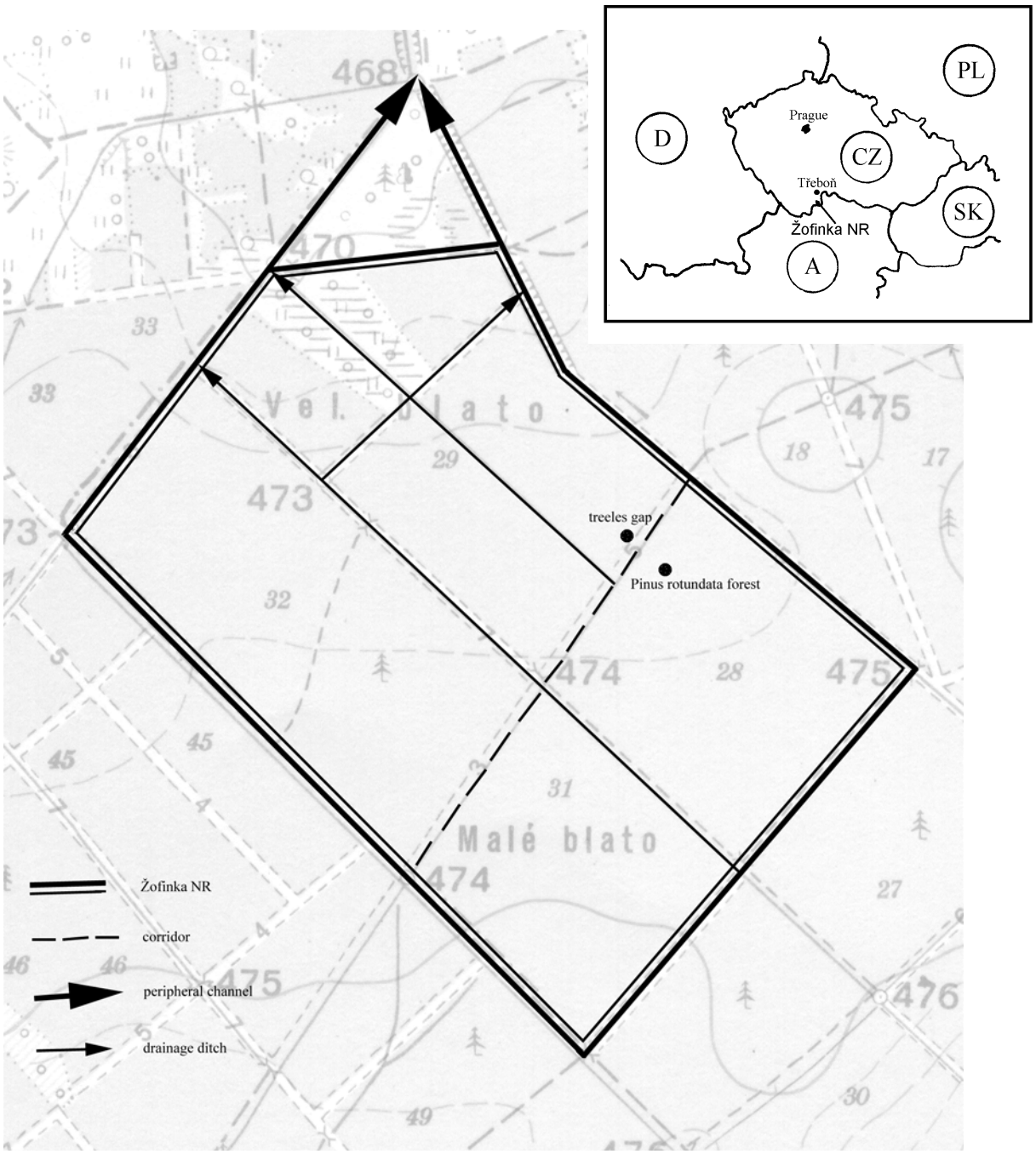

Fig. 1. a) Location of the study site – Žofinka Nature Reserve (48°49´N, 14°53´E), Třeboň Biosphere Reserve, Czech Republic. b) Basic map of the Žofinka Nature Reserve.

Hydrological measurements

Hydrological measurements were taken weekly throughout the hydrological years 1994–1998 in the "Žofinka" peat-bog. Water table fluctuations were recorded in perforated 1.5 m long polyvinyl chloride pipes inserted permanently in the peat. Twenty pipes were placed inside the peatbog. In this paper, water fluctuations of two sites in similar hydrological conditions (same peat depth, distance to the nearest ditch etc., Fig. 1b) are presented: (i) undisturbed *Pinus rotundata* forest (type 3 in Fig. 2) and (ii) primarily same stands, where most tree

canopy was removed by both insect infestation and local windthrows during the last 20 years; present vegetation is described in type 4 (Fig. 3).

Precipitation was sampled as bulk precipitation weekly. During the frost-free season rainfall amount was recorded directly in the "Žofinka" peat-bog using three rain gauges (type Hellman) situated inside the peat-bog. The upper edge of every rain gauge was situated 1 m above the ground surface and precipitation was measured with a 0.1 mm accuracy. For the frost period, precipitation data from the meteorological station in Třeboň were used.

Results

Previous vegetation of the 1970s

Vegetation map from 1977 (Fig. 2) and 16 relevés from 1971 (Table 1) made by Kučera (1977) illustrate the vegetation cover on the locality in the 1970´s.

The *Pinus rotundata* forest with *Ledum palustre* in undergrowth was the main vegetation type (type 3 in Fig. 2, relevé No. 4, 5, 6 and 15 in Table 1) in the central part of the "Žofinka" peat-bog in 1970´s. It consisted of relatively uneven-aged homogenous stands of *Pinus rotundata*, only with little admixture of *Pinus sylvestris* (max. 10%). The herb layer included ericoid dwarf shrubs (*Ledum palustre, Vaccinium myrtillus, V. vitis-idaea* and *V. oxycoccus*), the moss layer was dominated especially by *Sphagnum* species (e. g., *Sphagnum fallax* and *S. capillifolium*), *Dicranum polysetum, Polytrichum formosum* and *Pleurozium schreberi*.

A part of this vegetation type (type 3a) was influenced by preparation for peat extraction in the past (trees were cut down and removed), but without any disturbances of the peat surface. In 1971 these *Pinus rotundata* stands were young, trees were branched to the ground, somewhere canopy openings were present. Composition of both herb and moss layer was similar to the former type.

Towards the peat-bog edge *Pinus sylvestris* was more abundant, probably in relation to shallower peat layer. This type (type 4), known as natural pine bog forest (*Vaccinio uliginosi-Pinetum* Kleist, relevés No. 2 and 16), was dominated by *Pinus sylvestris* with undergrowth similar to that of the *Pinus rotundata* forest.

In the western, eastern and northern marginal parts of the reserve denser, artificial spruce forests occurred (type 1, relevés No. 7 and 13). According to species composition they were near to natural waterlogged spruce forest (e. g., *Calamagrostis villosa* participated in the herb layer and *Bazzania trilobata* in the moss layer), but still with higher admixture of *Pinus sylvestris*. Spruce forest near the NE drainage channel fringed out into a light, wet artificial pine forest, herb layer was occupied by *Molinia caerulea* (type 2, relevé No. 8).

The sites influenced by turf digging occurred in the northern part of the reserve (type 5, relevés No. 11 and 12). Peat was excavated there probably until the second half of 20th century. The sites were occupied by a complex of degradation stages of types No. 3 and 4. They comprised a mosaic of three vegetation types:

- dried stands of heathlike character on low ground elevations. Here self-regenerating stands of *Pinus rotundata, P. sylvestris* and mostly *P.* × *digenea* occurred, in the herb layer *Calluna vulgaris* dominated.
- wet stands in terrestrialised depressions dominated by *Betula pubescens, Pinus rotundata* and *P. sylvestris* in the tree layer and *Molinia caerulea* in the herb layer,
- deep depressions with open water, very rare. They originated from local deep turf digging.

Also other man-influenced types were present – stands on the corridor pathes (type No. 6 and 7). *Molinia caerulea* and some ericoid species dominated on the rarely used trails and along the drainage ditches (relevé No. 3). The frequently used, partly compacted pathes were vegetated by *Molinia caerulea, Avenella flexuosa, Poa annua* or *Deschampsia caespitosa*

(relevé No. 14). *Sphagnum* sp. dominated in the initial stages of terrestrialisation of drainage ditches (type 8, relevé No. 10).

Present vegetation in 1998

Vegetation in 1998 is described by the vegetation map (Fig. 3) and by 26 relevés (Table 2). Present vegetation has been strongly influenced by windbreaks which disturbed both central and marginal parts of the peat-bog during the summer and autumn of 1984. Windstorms created many small- and large-scale windthrows which became a food basis for infestation of bark-beetle. Consequently, break-up of the tree cover proceeded on most of the area of the locality. Especially the most valuable stands of the former *Pinus rotundata* forest have been strongly affected by both windbreaks and insects. Liška et al. (1989) found the large-scale attack of different species of wood endgraver on living trees of *Pinus rotundata*, however, most trees of *Pinus sylvestris* were without damage. A part of windthrows was destroyed by fire in spring 1994 (Kloubec et al. 1995).

In 1998, substitutive stands, replacing the previous *Pinus rotundata* forest, were the main vegetation type on the locality (type 4 in Fig. 3, relevés No. 4, 6, 8 14, 20, 23, 24 and 26). Different stages of new developing *Pinus rotundata* bog forest can be distinguish.

The advanced stages were in those stands where windthrows were frequent – numerous wet depressions were suitable for regeneration of the community. Low trees (up to 5 m) have already established, *Betula pendula* and *Frangula alnus* gradually retreated, *Pinus rotundata* or hybrids (*P.* × *digenea*) became dominant. Luxuriant herb layer consisted of ericoid dwarf shrubs (*Ledum palustre, Vaccinium myrtillus, V. uliginosum* and *V. vitis-idaea*). *Sphagnum flexuosum* or *S. fallax* and some dwarf shrubs (*Andromeda polifolia* and *Vaccinium oxycoccus*) occurred in wet depressions created by uprooted trees.

So far, dead trees, snags and scattered living trees of *Pinus sylvestris* could be found on sites that were disturbed mainly by gradation of insects. *Frangula alnus* and *Betula pendula* dominated on those sites, luxuriant herb layer consisted of a mosaic of ericoid dwarf shrubs. In the moss layer, *Sphagnum* species occurred in relation to the surface topography, xerophilous moss species (*Pleurozium schreberi*, *Dicranum scoparium*) were frequent. Young *Pinus rotundata* trees were found only occasionally.

On the burnt site (fire in 1994), vegetation cover regenerated rapidly (type 5, relevé 7). *Molinia caerulea* dominated there, as well as ericoid dwarf shrubs (especially *Ledum palustre*), *Betula pendula* and *Frangula alnus* scattered occurred. Bare peat was occupied by pioneer moss species (*Marchantia polymorpha, Pohlia nutans* and *Bryum palens*), weed species (e.g., *Sonchus arvensis, Taraxacum* sect. *Ruderalia*) and seedlings of *Salix caprea* or *Populus tremula*. The regeneration of moss layer was concentrated especially in wet depressions. Seedlings of *Pinus sylvestris* frequently occurred there.

Former *Pinus rotundata* forests (type 3, relevés No. 3, 9 and 25) persisted only in fragments. Tree cover was low, canopy openings were frequent and the abundance of *Pinus sylvestris* has increased. Species composition of herb and moss layer was similar to the former *Pinus rotundata* forest, dwarf shrubs dominated.

Stands of natural pine bog forest (*Vaccinio uliginosi-Pinetum sylvestris* Kleist, type 2, relevés No. 17 and 22) surrounded the central part of the bog. Most of them were not influenced by wind disturbance or insect infestation. *Pinus rotundata* trees were rare there, little admixture of *Picea abies* occurred in the tree layer. Some species characteristic for natural pine bog forest occurred in the undergrowth (*Ledum palustre, Vaccinium uliginosum, Sphagnum magellanicum* etc.).

The artificial spruce forests, 100–120 years old, occurred in the marginal parts of the reserve (type 1, relevés No. 12, 13, 17 and 18). Composition of the herb layer was similar to

natural waterlogged spruce forest, in the tree layer *Pinus sylvestris* was abundant. In the eastern and western part of the reserve many spruce trees were recently affected by yellowing of needles and their litterfall. Consequently, the trees died off, probably as a result of raised water table after damming of the central drainage ditch (in 1994).

Stands of *Molinia caerulea* together with some species from contact communities (mostly ericoid shrubs) were frequently distributed along the drainage ditches and trails (relevés No. 5, 15 and 16).

Young stands of *Pinus rotundata* and *P.* × *digenea* with admixture of *Pinus sylvestris* (40 years old) occurred in the northern part of the reserve, which was affected by turf digging in the past (type 7, relevés No. 10 and 11). Species composition of the herb and moss layer corresponded to the site hydrology – *Sphagnum* sp., *Molinia caerulea* and *Vaccinium uliginosum* predominated in wet depressions, ericoid shrubs (*Vaccinium myrtillus, Calluna vulgaris*) and more xerophilous mosses in drier parts.

Vegetation change and hydrological condition

Canopy break-up resulted in the environmental changes. Besides the changes in radiation environment and temperature amplitudes in the understory, also changes of hydrological conditions were remarkable.

Comparison of water table fluctuation in two sites for the period 1994–1998 is given in Fig. 4. Fluctuations of water table had a characteristic pattern during a year. Highest water table usually occurred in early spring after saturation of peat profile by melting snow. From the end of April (beginning of vegetation season), water table gradually decreased in both sites due to intensive evapotranspiration. In case of frequent or heavy rainfall (precipitation usually more than 30 mm per week) the water table started to rise and, for a short period, it could keep near its maximum (e. g., in July 1997). At the end of season the water table slowly approached bog surface and culminated according to the length of frost period during winter or early spring.

Treeles gap (full line) showed a smaller fluctuation of water table (mean water table depth 18.6 cm below ground) than the undisturbed *Pinus rotundata* forest (broken line, mean water table depth 25.5 cm below ground), especially during the vegetation period. By contrast, during winter and early spring the differences between both sites were negligible.

Remarkable differences in water table fluctuation are summarised in Fig. 5 where frequency histograms of water table level for both sites are given. Water table declined up to 60 cm below ground in the undisturbed *Pinus rotundata* forest in comparison with 33 cm below ground in the treeles gap. Water table occurred most frequent in range from 10 to 25 cm below ground in both sites – 88% and 61% of observation were in this range in treeles gap and in undisturbed *Pinus rotundata* forest, respectively. As evapotranspiration considerably affects bog water balance by depleting moisture content from the upper part of the peat profile, different evapotranspiration intensities are assumed to be responsible for the differences in water table fluctuations. Trees are more effective in water absorption from peat owing to deeper roots in comparison with carpets of *Sphagnum* sp. div., which depend especially on water diffusion and capillarity. Simultaneously, higher leaf area of stands dominated by trees than of those dominated by dwarf shrubs or by *Sphagnum* sp. div. determines their more intensive evapotranspiration.

Water table fluctuations in the central parts of the "Žofinka" peat-bog were close to that of the treeles gap in the 1990´s (mean depth 0–15 cm, maximum 20–30 cm, Koroš et al. 1998). We may suppose that the water table in the beginning of 1970´s (i. e., in time of *Pinus rotundata* forest´s dominance inside the bog and before excavation of peripheral channels) was rather similar to the water table of the undisturbed *Pinus rotundata* forest (Fig. 4, 5),

because of higher evapotranspiration. Destruction of the tree cover might induced a smaller water table fluctuation with many other consequences (changes in nutrient release, reduced peat decomposition, support of *Sphagnum* sp. growth, etc.).

Discussion

Vegetation maps from 1977 and 1998 (Fig. 2 and 3) illustrate the radical vegetation changes in the central part of the "Žofinka" peat-bog during the last 20 years. The previous *Pino rotundatae-Sphagnetum* community, only marginaly influenced by man in the past, was strongly affected by natural disturbances (wind, insect infestation and partly by fire).

Small-scale windbreaks or windthrows are characteristic in succession of peat-bogs forested by *Pinus rotundata* and play an important role in the community regeneration (Neuhäusl 1972). However, the magnitude of vegetation changes on the locality is indicative of preceding reduction of tree fitness and, consequently, of their low stability.

When the declaration of the "Žofinka" Nature Reserve being prepared the local Forest Administration proposed an excavation of drainage ditches inside the peatbog and, consequently, pine and spruce plantation. After several discussions a compromising solution was adopted, i. e. "only" deep drainage channels were made on the edges of the reserve in 1970´s as a protection of surrounding spruce and pine plantations against soil wetness. According to the hydrological measurements made by Koroš et al. (1998) drainage range of the channels is up to 50 metres, therefore the peripheral channels strongly influence only the marginal parts of the reserve where water table can decrease up to 90 cm below ground. The central part is more affected by shallow ditches which drain water in the active layer (acrotelm). However, increasing drainage of the central part of the reserve may be supposed after excavation of peripheral channels in 1970´s, especially through central drainage ditches because of their direct connection with the peripheral channels. As the *Pinus rotundata* trees usually develop horizontal shallow roots the presumed decrease of water table could reduce tree fitness during drier periods (Schweingruber 1996, p. 137).

Increase of growth potential of trees (increase of both tree height and tree ring width) in peat-bogs after drainage has been reported by several authors (e.g., Grünig 1955, Schmidt et al. 1995 etc.). However, successive disproportions between the height of trees (up to 14 m) on drained peatbog and shallow root system (often limited to 20–40 cm below ground owing to higher water table in some periods of year and toxic conditions in deeper peat layers) could diminish stability of trees on unstable peat soils and increase the probability of windbreaks.

The *Pino rotundatae-Sphagnetum* community and related communities are close to the northern taiga ecosystem (c. f., Neuhäusl 1972, Rektoris 1994). Abrupt vegetation changes or catastrophic disaster (heavy windstorms, insect infestation and fire) are considerable features of coniferous forests (Frelich et Reich 1995). Evidences of periodic fire disturbances of community dominated by *Pinus rotundata* were found by Jankovská (1980) in the "Červené blato" Bog in charcoal layers in peat sediments. From this point of view, the abrupt canopy break-up described above is only one stage of natural succession in this type of ecosystem. The importance of canopy break-up to the cyclic regeneration of the community is stressed also by Neuhäusl (1972).

Vegetation mapping has shown that the natural regeneration proceeds in different successional pathways in stands disturbed by wind and in those affected by insect infestation. Regeneration of the *Pinus rotundata* forest is successfull on stands with windthrows as a result of (i) acceleration of the growth of understory individuals after canopy break-up and (ii) of more favourable conditions for germination and growth of seedlings in shallow wet depressions formed by uprooted trees. Also studies on germination, establishment and growth

of young *Pinus rotundata* plants made by Schmidt et al. (1995) showed that both germination and survival of seedlings were more successfull in wet conditions, further light was found an important factor for the regeneration of the species.

By contrast, dead trees and snags were typical for stands affected by insect gradation. When a dead tree falls down only a bottom part of the trunk breaks off without formation of any windthrow. Consequently, suitable habitats for seedling growth are missing. Also most of understorey *Pinus rotundata* trees were damaged during the insect infestation resulting in a recent invasion of pioneer tree species (*Betula pendula* and *Frangula alnus*) on those sites.

Canopy break-up may further support genetic erosion of *Pinus rotundata* due to hybridisation with *Pinus sylvestris* (*P. rotundata* × *P. sylvestris* = *P.* × *digenea*), which Businský (1998) reported for peatbogs in the Třeboň Basin. Monitoring of the extent of hybridisation in different vegetation types is under study now.

Response of the spruce stands in the NW part of the reserve to the damming of drainage ditch is important for management purposes. Abrupt elevation of water table reduced tree fitness, consequently resulting in their quick dieback. In the case of next manipulation of water table special attention should be given to the ability of established tree cover to adapt to new hydrological conditions.

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Změny vegetace v NPR Žofinka na Třeboňsku

Změny vegetačního krytu v NPR Žofinka na Třeboňsku za posledních 20 let byly hodnoceny na základě mapy aktuální vegetace Dr. S. Kučery z r. 1977 (obr. 2) a na základě námi provedeného mapování aktuální vegetace v r. 1998 (obr. 3).

Podle dosud nepublikovaného materiálu Dr. S. Kučery představovalo blatkové vrchoviště Žofinka na začátku 70. let lidskou činností málo narušené a geneticky nejstabilnější blatkové bory na Třeboňsku (as. *Pino rotundatae-Sphagnetum* Kästner et Flössner 1933, corr. Neuhäusl 1972). Během posledních 20 let však původní blatkové porosty z velké části podlehly přirozené disturbanci (větrná kalamita v r. 1984, následný rozvoj podkorního hmyzu a na části lokality požár v r. 1994). V současné době představují hlavní vegetační typ centrální části rašeliniště degradační stádia rozpadu blatkových borů a jejich náhradní porosty v různém stupni a směru sukcese. Na části lokality, ovlivněné především rozvojem podkorního hmyzu, se objevují porosty s dominantními pionýrskými dřevinami (*Betula pendula* a *Frangula alnus*) a absencí borovice blatky.

Odstranění stromového patra mělo pozitivní vliv na rozvoj porostů erikoidních keříků a vedlo také ke změnám hydrologických podmínek na lokalitě, především ke snížení kolísání hladiny podzemní vody, které dokumentují obr. 4 a 5.

Podle aktuálního stavu vegetace lze konstatovat, že na větší části původní rozlohy blatkových porostů dochází k jejich obnově, která by při dostatečném zvodnění stanovišť měla úspěšně pokračovat. Otázkou zůstává, do jaké míry se na naznačeném vývoji podílelo prohloubení obvodových kanálů a odvodňování lesních porostů v okolí lokality v 70. letech.

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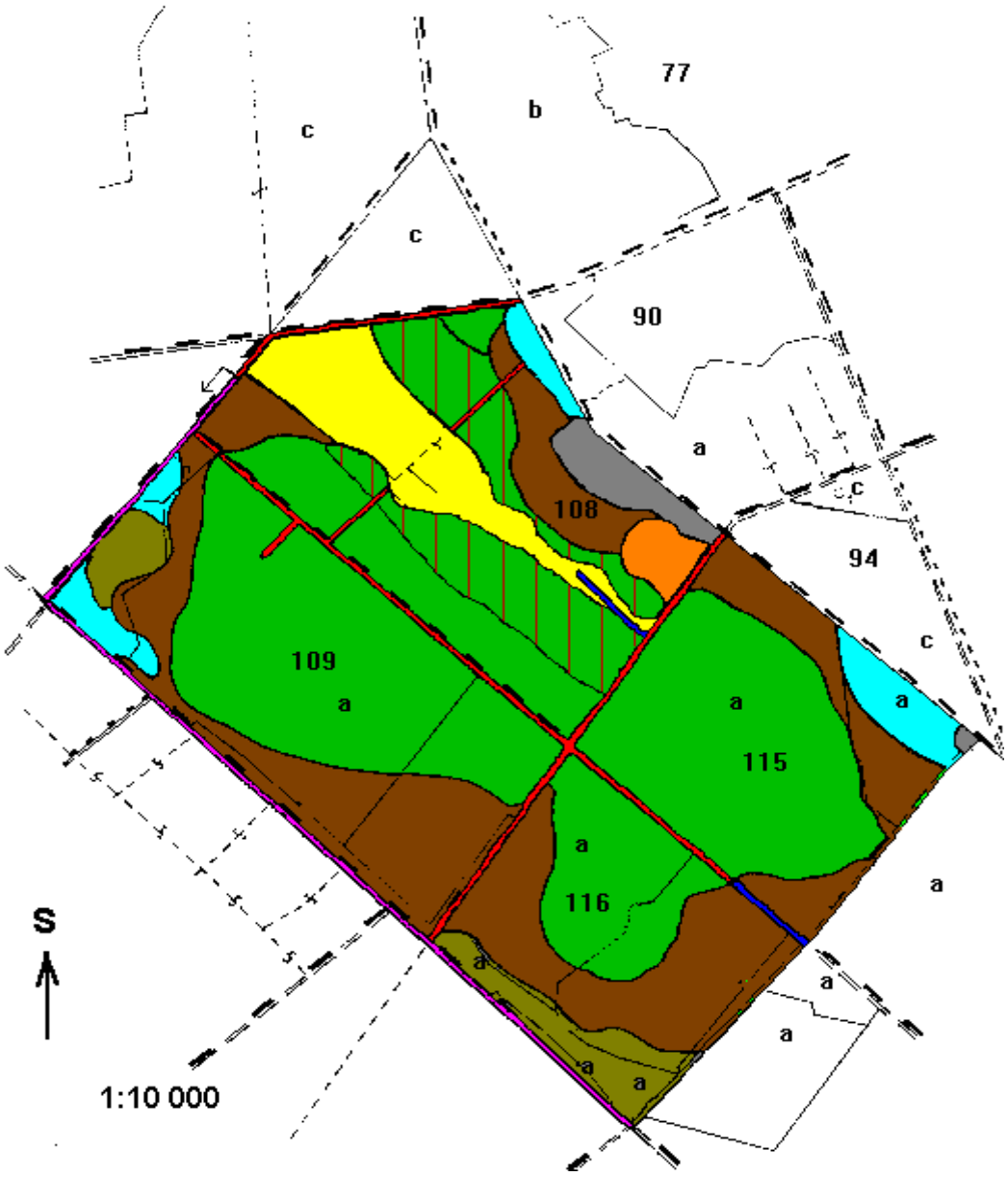


Fig. 2. Actual vegetation map from 1977 made by Kučera (1977).

Legend

1

Artificial spruce plantation, mostly younger, near to natural waterlogged spruce forest with higher admixture of *Pinus sylvestris.*

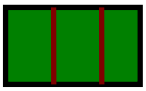
2

Artificial pine forest with abundant *Molinia caerulea*. Homogenous stands, very wet.

3

Pinus rotundata forest with *Ledum palustre* in undergrowth – homogenous stands on deeper peat (2–4 m), max. admixture of *Pinus sylvestris* up to 10%. The best stands in central and western part of the compartment No. 115 and in centre of the compartment No. 119.

3a



Sites, which were prepared to turf cutting by clearance, peat surface stayed intact. Tree cover self-regenerated. *Pinus rotundata* forest was younger, very dense and crowded up to bottom, somewhere more open. E_1 was like in the type No. 3.

4

Natural pine bog forest dominanted by *Pinus sylvestris*, boundary between types No. 3 and 4 not strong, it was rather soft transition following reduction of peat depth.

Probably only the succesional stage of the type 4. Stands were younger, very dense, even-aged and assumedly of artificial origin. E_1 was like in the type 4.

Analogous stands to the typ 3a, but more open (somewhere *Calluna vulgaris* stage). A transition to turf digging sites (type 5). Peat surface intact, without turf digging.

5

Complex of degradation stages of types 3 and 4 on turf digging sites. Three main types:
– dried habitats in sites with shallow turf digging, self-regenerating stands of *Pinus rotundata* and *P.* × *digenea,* in the herb layer *Calluna vulgaris*,
– wet habitats in terrestrialisated depressions after turf digging, vegetated by *Molinia caerulea-Betula pubescens- P.* × *digenea* et *sylvestris*,
– small deeper depressions – result of local turbaries, rarely open water.

6

Molinia caerulea and some ericoid species dominated on the rare used trails and along drainage ditches.

7

Stands of grasses on frequently used corridor pathes, usually in combination of previous type.

8

Initial stage of terrestrialisation of drainage ditches, somewhere open water.

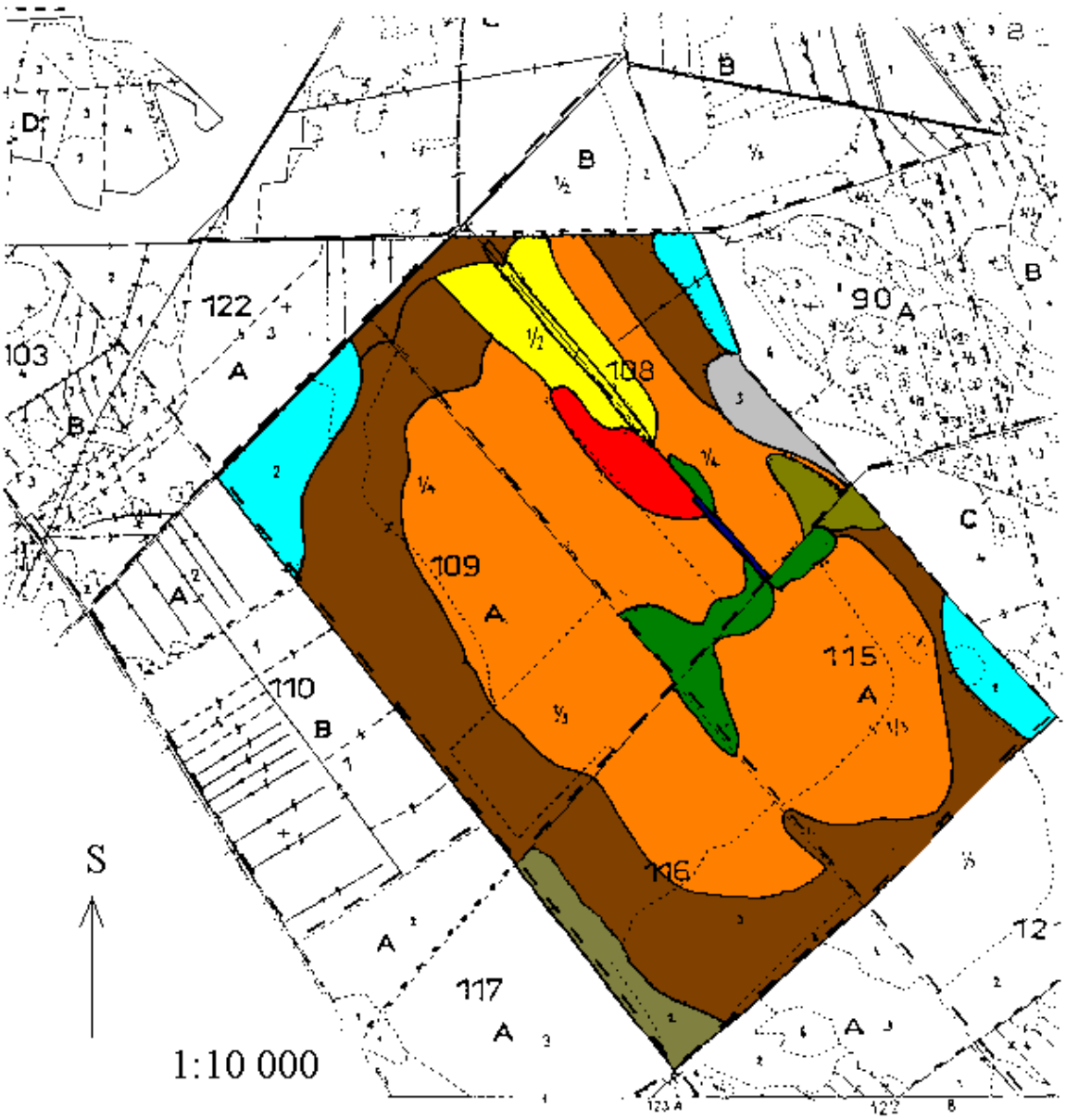


Fig. 3. Actual vegetation map from 1998.

Legend

1

Artificial spruce plantation, age of 100-120 years, close to natural waterlogged spruce forest with higher admixture of *Pinus sylvestris*

Molinia caerulea stands with scattered pine trees. Deadwoods and snags very frequent, waterlogged sites.

2

Natural pine bog forest dominanted by *Pinus sylvestris*, ericoid dwarf shrubs dominate in the herb layer.

3

Former *Pinus rotundata* forest with *Ledum palustre* in undergrowth – only fragments on deeper peat.

Young stands of *Pinus rotundata*, branched to the ground. It is a transition stage to the type 7, without any disturbance of peat surface.

Managed pine forest with several species characteristic for *Pinus rotundata* forest (e.g. *Ledum palustre*)

4

Stands disturbed by windbreaks or by expansion of wood engraver. Tree layer has started to regenerate – more or less sparse stands of *Pinus rotundata, Pinus* x *digenea* or *Frangula alnus* and *Betula pendula*. Mosaic of ericoid shrubs and *Molinia caerulea* in the herb layer.

5

Site affected by fire in 1994, in the herb layer *Molinia caerulea* dominated, ericoid dwarf shrubs scattered occurred, E_0 regenerated in wet depressions.

6

Initial stage of terrestrialisation of drainage ditches, somewhere open water

7

Stands affected by peat digging, in the tree layer a mixture of *Pinus rotundata, P.* x *digenea* and *P. sylvestris* dominated.

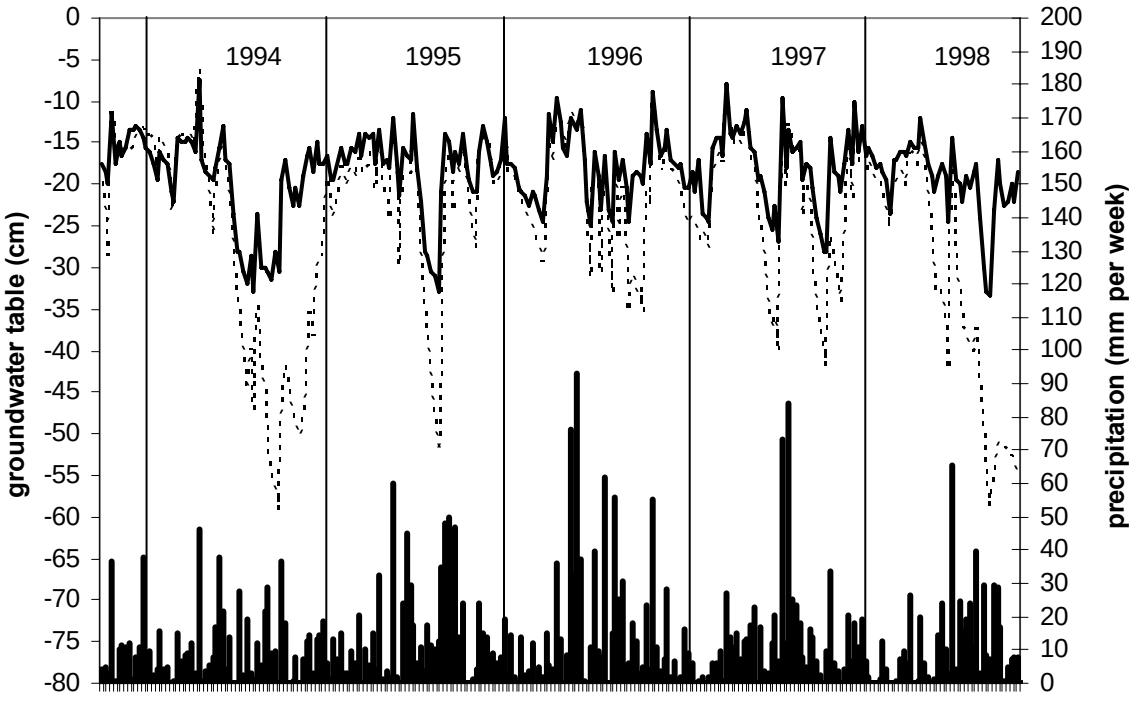


Fig. 4. Water table courses in two sites during the period 1994–1998 and weekly sums of precipitation. Full line – treeles gap, i.e. the stand strongly affected by both windthrows and insect infestation, dwarf shrubs dominated, only scattered *Pinus rotundata* trees occurred; broken line – undisturbed *Pinus rotundata* bog forest; vertical bars – weekly sums of precipitation.

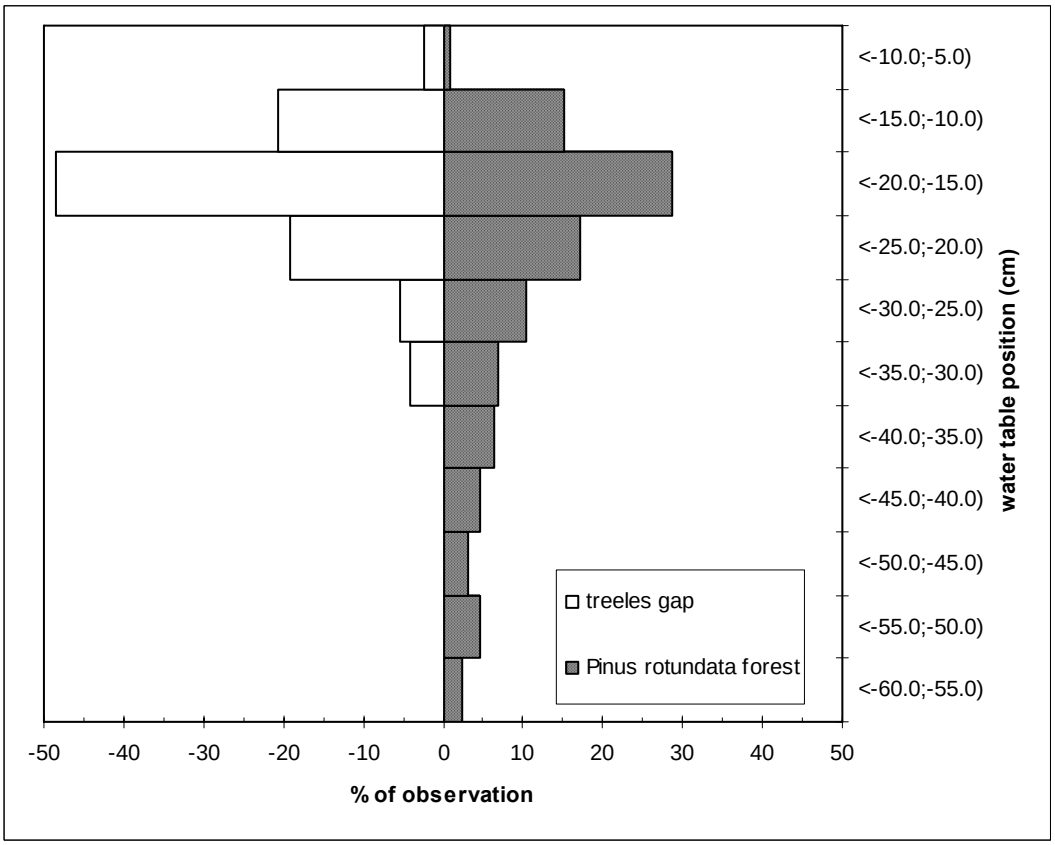


Fig. 5. Frequency histograms of water table level in two sites during 1994–1998. 1 – treeles gap, 2 – undisturbed *Pinus rotundata* bog forest.

Table 1: Phytosociological relevés recorded by Kučera (1977) in 1971. P – only presence of species was recorded (relevé No. 5).

Relevé number	7	13	8	4	5	6	15	1	2	16	9	11	12	14	3	10
Year ..	71	71	71	71	71	71	71	71	71	71	71	71	71	71	71	71
Month	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Day	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14
Relevé area (m2)	500	250	300	500	500	500	500	500	500	500	300	300	300	6	6	6
E3 (%)	97	97	90	90	80	85	90	90	85	90	80	0	3	0	0	0
E2 (%)	0	0	3	15	10	10	10	15	25	15	35	15	20	0	0	0
E1 (%)	30	15	97	95	97	97	97	95	93	97	97	98	85	100	100	2
E0 (%)	40	30	75	97	98	98	98	97	95	98	75	15	20	0	65	95
No. of species	18	18	20	29	32	27	30	24	30	36	24	19	21	11	11	4
E3 upper																
Pinus sylvestris	3	4	5	.	.	.	.	5	.	.	2	1	.	.	.	.
Picea abies	5	3	.	.	.	.	.	2	.	.	1	.	.	.	.	.
Betula pubescens	.	.	.	.	.	.	.	1	.	.	+	+	+	.	.	.
Pinus rotundata	.	.	.	.	.	.	.	.	.	.	4	1	1	.	.	.
E3 middle																
Pinus sylvestris	.	.	.	1	1	1	1	.	4	4	.	.	.	.	.	.
Pinus rotundata	.	.	.	5	5	5	5	.	2	2	.	.	.	.	.	.
Picea abies	.	.	.	.	+	.	+	.	1	2	.	.	.	.	.	.
E3 lower																
Pinus rotundata	.	.	.	2	3	3	1	.	2	+	.	.	.	.	.	.
Picea abies	.	.	.	1	+	+	1	.	+	2	.	.	.	.	.	.
Betula pubescens	.	.	.	+	.	.	.	.	1	+	.	.	.	.	.	.
Pinus sylvestris	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
E2																
Picea abies	.	.	1	1	+	+	1	2	1	2	.	.	.	.	.	.
Betula pubescens	.	.	+	+	.	.	+	1	+	+	+	.	+	.	.	.
Frangula alnus	.	.	+	1	1	+	+	1	2	1	.	.	.	.	.	.
Pinus rotundata	.	.	.	2	2	2	2	.	+	+	3	2	2	.	.	.
Pinus sylvestris	.	.	.	.	.	.	.	.	.	+	.	1	1	.	.	.
Sorbus aucuparia	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
E1																
Dryopteris carthusiana	+	+	1	1	1	.	+	2	+	+	.	.	.	.	.	.
Molinia caerulea	+	3	4	2	2	r	+	3	+	+	2	4	3	2	4	+
Vaccinium myrtillus	2	+	3	3	3	3	3	4	3	3	2	2	.	.	2	.
Vaccinium vitis-idaea	1	1	2	2	2	2	2	3	2	2	2	2	1	.	1	.
Calluna vulgaris	.	.	.	2	.	+	+	2	+	2	4	3	4	.	+	.
Ledum palustre	.	.	+	3	4	4	3	+	3	3	3	1	1	.	.	.
Lycopodium annotinum	.	.	.	.	r	.	.	+	.	+	.	.	.	.	.	.
Avenella flexuosa	3	2	+	2	2	1	.	3	2	2	2	.	.	2	2	.
Oxalis acetosella	.	.	.	.	r	r	.	+	+	.	.	.	.	.	.	.
Vaccinium uliginosum	.	.	.	1	+	1	+	.	2	+	2	+	+	.	+	.
Vaccinium oxycoccus	.	.	.	2	2	2	1	.	.	1	.	.	.	.	.	+
Epilobium angustifolium	.	.	.	r	r	.	.	.	.	+	.	.	.	.	.	.
Andromeda polifolia	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Calamagrostis villosa	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex rostrata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Eriophorum vaginatum	.	.	.	.	.	.	+	.	.	.	.	+	2	.	.	.
Carex nigra agg.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Eriophorum angustifolium	.	.	.	.	.	.	.	.	.	.	.	+	2	.	.	.
Agrostis capillaris	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.

Relevé number	7	13	8	4	5	6	15	1	2	16	9	11	12	14	3	10
Poa annua	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.
Stellaria graminea	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
Deschampsia cespitosa	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
Carex leporina	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Potentilla erecta	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Juncus conglomeratus	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Rumex acetosela s.lat.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Nardus stricta	.	.	.	.	.	.	.	.	.		.	.	.	+	.	.
seedlings										+						
Picea abies	.	.	+	+	+	.	1	1	1	1	.	.	.	.	.	.
Frangula alnus	r	+	1	.	1	+	+	1	1	+	+	.	.	.	.	.
Pinus rotundata	.	.	.	+	1	1	1	.	+	.	1	1	1	.	.	.
Sorbus aucuparia	.	.	r	.	.	.	.	.	r	+	.	.	.	.	.	.
Betula pubescens	.	.	.	.	r	.	.	.	.		+	.	+	.	.	.
Pinus sylvestris	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Quercus petraea agg.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
E0																
Leucobryum glaucum	2	.	2	.	.	.	+	2	2	+	2	.	.	.	.	.
Polytrichum formosum	3	2	3	3	P	2	3	2	3	2	3	.	.	.	.	.
Pleurozium schreberi	2	3	4	2	P	2	2	3	3	2	4	.	2	.	2	.
Dicranum polysetum	1	2	4	3	P	2	3	3	3	3	3	.	.	.	2	.
Sphagnum sp.	1	.	.	.	.	.	.	3	.	.	.	.	1	.	.	.
Sphagnum fallax	4	.	3	4	P	4	4	2	.	3	2	3	.	.	.	5
Sphagnum capillifolium	.	.	.	3	P	3	3	3	2	3	2	.	.	.	3	.
Hylocomium splendens	.	.	.	2	P	+	+	.	+	+	.	.	.	.	2	.
Polytrichum juniperinum	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Sphagnum girgensohnii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.
Polytrichum strictum	.	.	2	+	P	2	+	.	.	.	2	+	2	.	.	.
Cladonia sp.	.	.	.	+	P	+	.	.	.	.	.	.	3	.	.	.
Plagiothecium sp.	.	1	+	.	P	.	.	.	.	.	.	.	.	.	.	.
Bazzania trilobata	3	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Dicranum scoparium	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scapania sp.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum russowii	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Polytrichum commune	.	.	.	.	.	.	.	.	.	.	.	+	3	.	.	.
Dicranum sp.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Bryum sp.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.
Pohlia nutans	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hepatica sp.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 2: Phytosociological relevés recorded in 1998.

Relevé number	12	13	18	2	17	21	22	1	19	3	9	25	4	6	8	14	20	23	24	26	7	5	15	16	10	11
Year 19..	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98	98
Month	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08
Day	05	05	06	05	06	06	06	05	06	05	05	06	05	05	05	05	06	06	06	06	05	05	05	05	05	05
Relevé area (m2)	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	6	9	15	400	400
Slope (degrees)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E3 (%)	30	35	75	35	30	45	30	2	3	50	5	50	3	5	5	3	35	15	2	0	0	0	0	0	35	40
E2 (%)	15	5	3	40	10	5	20	10	5	10	35	10	40	30	20	30	5	25	30	30	5	0	5	0	5	10
E1 (%)	60	50	5	60	60	65	70	90	65	40	50	60	80	80	70	65	70	80	70	60	80	60	80	70	70	40
E0 (%)	40	60	15	50	80	60	50	80	85	40	60	40	60	50	65	60	80	80	75	65	40	95	30	80	70	40
Height of tree layer	20	25	-	12	-	20	16	10	-	8	-	10	-	-	15	-	-	7	-	6	-	-	-	-	10	7
No. of species	33	33	17	34	32	30	32	30	21	35	39	33	38	31	34	36	32	38	30	25	39	3	19	3	27	24
E3																										
Pinus sylvestris	2a	+	2b	2b	2b	2b	2b	1	+	1	.	2a	1	1	1	+	2b	2a	+	.	.	.	.	.	1	2a
Picea abies	1	2b	3	1	1	2b	+	+	.	+	1	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.
Betula pendula	+	.	.	+	.	+	.	.	.	+	.	1	.	.	.	.	+	.	.	.	.	.	.	.	+	.
Pinus x *digenea*	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	2a	.	.	.	.	.	.	.	2b	2b
Pinus rotundata	.	.	.	.	.	.	+	.	.	.	+	2b	1	+	.	+	.	+	.	.	.	.	.	.	.	.
Sorbus aucuparia	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
E2																										
Frangula alnus	2a	1	.	3	1	1	2a	2a	+	1	2a	1	3	2a	1	1	+	2a	1	+	1	.	1	.	r	+
Betula pendula	+	+	.	1	+	+	1	2a	+	+	1	1	1	+	1	1	+	1	2a	1	+	.	+	.	.	+
Pinus sylvestris	.	.	.	.	1	.	+	1	1	.	+	+	+	r	1	1	1	1	2a	1	.	.	.	.	1	1
Sorbus aucuparia	r	.	.	r	.	.	+	+	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.
Picea abies	+	1	+	+	+	+	+	.	.	.	1	.	+	+	+	1	+	+	+	.	r	.	.	.	.	.
Pinus x *digenea*	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	1	2a	2b	.	.	.	.	1	1
Pinus rotundata	.	.	.	.	.	.	.	.	.	.	2a	1	1	+	2a	2a	.	.	.	.	+	.	.	.	.	.
E1																										
Molinia caerulea	+	+	+	1	+	+	+	5	3	+	1	+	1	2a	1	+	+	+	1	+	3	+	3	3	3	1
Vaccinium myrtillus	3	3	1	3	3	3	3	2a	1	3	2a	3	3	3	2b	3	2b	3	3	3	1	.	1	.	2b	2a
Vaccinium vitis-idaea	1	+	+	+	1	1	1	1	+	2a	1	1	2b	2a	1	+	1	1	1	1	1	.	.	.	+	+
Vaccinium uliginosum	.	.	.	+	.	.	1	1	+	+	1	+	2b	1	1	+	2b	.	1	2b	+	.	2a	.	1	1

Relevé number	12	13	18	2	17	21	22	1	19	3	9	25	4	6	8	14	20	23	24	26	7	5	15	16	10	11
Ledum palustre	1	.	.	2a	2b	+	2a	1	2b	1	2b	2b	2b	2b	3	2a	4	3	3	2b	2b	.	2a	.	1	2b
Dryopteris carthusiana	+	+	.	+	+	+	+	1	.	+	1	+	1	1	1	+	+	+	+	+	.	.	+	.	+	.
Avenella flexuosa	1	1	+	1	1	+	+	.	.	1	1	+	1	.	+	1	+	+	+	.	.	.	+	.	.	.
Calluna vulgaris	+	.	.	+	.	+	1	.	.	1	1	1	2a	1	1	+	.	+	1	+	2a	.	.	.	+	2a
Stellaria longifolia	.	.	.	+	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	r	.	+	.	.	.
Andromeda polifolia	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.	.	.	.	.	.	.	.	.	.	.
Vaccinium oxycoccus	.	.	.	.	.	.	.	.	.	.	+	.	+	.	1	1	+	+	.	2a	+	.	.	.	+	.
Eriophorum angustifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.
Epilobium angustifolium	.	.	.	.	.	.	r	.	.	.	+	.	.	+	.	.	.	+	.	.	+	.	.	.	.	.
Eriophorum vaginatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	+	.	.	.	1	+
Gnaphalium sylvaticum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Dryopteris dilatata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Hieracium pilosella	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Oxalis acetosella	+	.	.	.	+	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Lycopodium annotinum	1	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stellaria alsine	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Carex rostrata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	.
Seedlings																										
Pinus sylvestris	+	.	.	.	+	r	+	+	+	+	+	+	+	.	+	.	.	+	+	+	+	.	.	.	+	+
Picea abies	+	1	.	+	+	+	+	+	.	+	+	+	r	r	.	+	.	+	.	.	.	.	r	.	.	.
Sorbus aucuparia	+	r	.	+	.	.	+	+	.	+	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Frangula alnus	1	1	.	+	1	+	+	.	+	2m	1	+	2a	1	1	+	+	+	+	+	+	.	+	.	+	+
Betula pendula	.	+	.	+	+	.	.	.	.	.	+	+	.	+	1	.	.	+	+	+	+	.	.	.	.	.
Betula pubescens	.	.	.	+	r	.	.	.	.	.	.	+	r	.	.	+	.	.	.	.	r	.	.	.	.	.
Quercus robur	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinus sp.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix aurita	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Quercus sp.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix caprea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Populus tremula	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+	.	.	.	.	.
Sonchus arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
E0																										
Pleurozium schreberi	2a	1	1	2b	+	2a	1	2a	+	2a	1	2a	2b	2b	2a	1	1	1	1	1	.	.	+	.	+	1
Sphagnum capillifolium	1	2b	+	3	3	2b	2b	1	.	3	.	.	3	1	2a	.	2a	2b	2b	.	.	.	1	.	.	1

Relevé number	12	13	18	2	17	21	22	1	19	3	9	25	4	6	8	14	20	23	24	26	7	5	15	16	10	11
Sphagnum fallax	1	+	.	.	.	1	.	3	2b	1	2a	2a	2a	.	2a	2a	3	2b	2a	2b	2b	5	.	5	3	2a
Sphagnum fimbriatum	.	.	.	.	.	.	.	2a	4	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	+	.
Lepidozia reptans	.	+	+	.	.	.	.	1	.	.	+	.	.	r	.	+	.	+	+	.	.	.	.	.	.	.
Dicranodonti denudatum	.	+	.	r	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tetraphis pellucida	+	+	+	1	+	+	+	1	.	1	+	+	+	r	+	+	+	+	+	+	+	.	.	.	.	.
Polytrichum commune	+	1	.	+	.	.	.	1	.	+	+	+	+	+	+	+	+	.	.	+	+	.	+	.	+	.
Polytrichum strictum	.	.	.	+	+	.	.	+	+	+	.	.	+	+	+	.	.	+	.	.	1	.	.	.	+	+
Dicranella cerviculata	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	+	r	.	.	.	+	.
Sphagnum flexuosum	.	.	.	.	.	.	.	2a	.	1	2a	.	2a	2a	2a	2a	2a	2a	2a	2a	1	.	.	.	2a	.
Pohlia nutans	+	+	.	+	+	.	+	1	+	.	+	+	+	.	+	+	+	+	+	+	+	.	.	.	+	+
Plagiothecium laetum	+	+	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Sphagnum magellanicum	.	.	.	1	2a	1	1	1	1	+	2b	2a	2b	2b	2a	3	1	3	2b	2b	2a	.	.	.	1	1
Dicranum polysetum	1	2b	1	2a	1	2a	1	r	+	1	1	1	2a	1	1	1	1	1	1	1	.	.	.	.	.	.
Dicranum flexicaule	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicranella heteromalla	.	+	.	.	+	+	.	.	+	+	+	+	+	.	.	.	+	+	.	+	r	.	.	.	+	+
Mylia anomala	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r
Sphagnum russowii	+	1	.	.	.	+	.	.	.	r	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.
Leucobryum glaucum	1	1	+	2a	2a	2a	+	.	.	2a	+	1	.	.	.	+	.	+	.	.	.	.	.	.	.	1
Sphagnum girgensohnii	.	.	.	1	2a	.	.	.	2a	1	.	.	1	.	.	.	.	.	.	.	.	.	2a	.	.	.
Orthodicranu flagellare	+	+	.	+	+	+	.	.	.	.	+	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.
Aulacomnium palustre	.	.	.	.	.	+	.	.	.	.	+	.	1	+	+	+	+	+	+	.	+	.	.	.	.	.
Bazzania trilobata	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Brachythecium sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Campylopus introflexus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Cephalozia connivens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.
Dicranum scoparium	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hylocomium splendens	+	.	.	1	.	+	1	.	.	.	+	.	.	.	.	+	.	.	+	.	.	.	1	.	.	.
Hypnum cupressiforme	.	r	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Lophocolea bidentata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.
Lophocolea heterophylla	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Marchantia polymorpha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Orthodicranum montanum	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichum formosum	1	+	+	.	+	+	+	.	+	.	.	1	.	.	.	+	.	+	.	.	.	.	.	.	.	.
Polytrichum juniperinum	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.

RETENTION ABILITY OF BOG PINE PEAT BOG ECOSYSTEM AND ITS RESPONSE TO DOWNPOUR PRECIPITATION

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Introduction

Hydrological functions of mires are often connected with the widespread idea about bogs being like a big mushroom, catching and absorbing rainfall water, and, then in the dry period, supplying brooks and smoothing stream flows. One of the aims of this study was to explain that bogs are not simply a big water reservoir, but that water retention has similar rules in raised bogs as in other types of ecosystems.

The composition of peat soil and its physical features are the bases for the hydrology and retention ability of every bog ecosystem. The properties of the surface peat horizons differ greatly from those of the permanently anaerobic deeper peat. Ingram (1978) introduced the terms acrotelm and catotelm for the surface and lower horizon, respectively. When *Sphagnum* peat decomposes and becomes compacted, its hydraulic conductivity decreases rapidly (Rycroft *et al.* 1975). Changes in physical structure of the peat can reduce hydraulic conductivity by three to four orders of magnitude, from the surface to the base of the acrotelm (Ivanov 1975). In actively growing raised bogs, a surface layer with high hydraulic conductivity overlies the compacted peat which comprises most of the peat mass. Water movement through this dense peat layer, which is saturated with water, is particularly slow, with practically all surplus water flowing laterally through the acrotelm. This situation is similar to the groundwater mounds occurring in clays and other fine-textured deposits (Marino 1974). The thickness of the acrotelm varies from over 50 cm in many hummocks to less than 10 cm in hollows (Damman 1986).

Methods

Hydrological measurements were taken weekly throughout the hydrological years 1994-1998 in the Červené blato bog. Groundwater table fluctuations were measured in perforated 1.5 m long polyvinyl chloride pipes permanently inserted in the peat and closed with a rubber stopper above the peat surface. About 40 pipes were inserted into four different vegetation types of the peat bog: (i) regenerated site, (ii) undisturbed bog pine forest, (iii) disturbed bog pine forest, and (iv) spruce forest.

The water outflow measurements were taken weekly in two drainage ditches constructed ca 200 years ago. The ditches are about 1 m deep, partly overgrown by a *Sphagnum* carpet. In each ditch, one V-notch weir (type Thompson) was constructed for estimation of water discharge.

Precipitation was sampled as bulk precipitation weekly. During the frost-free season, rainfall was recorded directly in the Červené blato bog using three rain gauges (type Hellman) at each of three sites in the bog; parallel data were averaged. The upper edge of every rain gauge was situated 1 m above ground surface and the precipitation was measured with a 0.1 mm accuracy. For the frost period, the precipitation data from the nearest meteorological station in Třeboň (19 km to the North) were used.

Site description

The study site (331 ha) is located in the southern part of the Třeboň basin Biosphere Reserve in the Czech Republic, 19 km south of Třeboň. The Červené Blato bog (48°52´N, 14°48´E, 465–475 m a. s. l.) is a continental raised bog (so called Waldhochmoore, sensu Neuhäusl 1984) with natural stands of Bog pine (*Pinus rotundata*) and its hybrid with Scots pine (*Pinus* × *digenea*). A detail description of the vegetation dynamics of the locality is given by Rektoris (in press).

The association *Pino rotundatae-Sphagnetum magellanicii* Kästner et Flössner 1933 corr. Neuhäusl 1968 represents the current stage in the peat bog´s development (so-called bog pine forest). There are some stages of community development dependent on the depth to the groundwater table, age of trees, and degree of peat decomposition. The herb layer at the site consisted of ericoid species e. g., *Andromeda polifolia, Calluna vulgaris, Ledum palustre*, *Oxyccocus palustris, Vaccinium myrtillus, V. uliginosum* and *V. vitis-idaea*. Also present are the graminoids *Molinia coerulea, Eriophorum vaginatum* and *E. angustifolium* in the herb layer, and *Sphagnum magellanicum*, *S. angustifolium, S. capillifolium* and *S. flexuosum* in the moss layer.

A part of the bog was disturbed by peat extraction in the last century. After termination of peat extraction, the pits were flooded by water and conditions for new peat accumulation were created. A community, with *Sphagnum recurvum* and *Eriophorum vaginatum* (ass. *Eriophoro vaginati-Sphagnetum recurvi* Hueck 1925), dominates in those stands (so-called regenerated site).

Mean annual temperature is above 7 °C over the Třeboň basin area (Přibáň *et al.* 1992) and average temperature for vegetation season (April-September) is about 14 °C. Total annual precipitation is about 600–650 mm. Precipitation in the summer is appreciably greatly (400–450 mm) than in winter period.

Results

During the vegetation season, the response of the bog to precipitation depends especially on the actual position of the groundwater table. In Fig. 1 the exponential relationship between water discharge and groundwater table level in the bog pine forest, during the vegetation seasons 1995-1998, is shown. It is evident that water discharge starts at the groundwater level about 30 cm below the surface. Until this position of the groundwater table is reached, most of the rainfall water accumulates in the peat profile and water discharge is small or zero. The same is true for the regenerated site, only the starting level for discharge is near the ground surface (about 4 cm below ground surface).

In winter, after the bog freezes, precipitation (snow) will accumulate on the surface rather than recharge the bog water reservoir, causing the groundwater table to slowly decrease. In the case when winter precipitation comes in the form of rain (sometimes during short episodes of warm weather), and the bog remains frozen, the rain water will not accumulate, and most of it will outflow from the bog surface (*e. g.*, in the 1995, December 25 in Tab. 1). When winter weather is very mild, the highest groundwater table will already occur during winter. If the frost period continues the whole winter, melting snow will saturate the peat profile during early spring.

Examples of bog responses, i. e., changes of groundwater table and water discharge to total precipitation amounts for selected weeks, are given in Tab. 1.

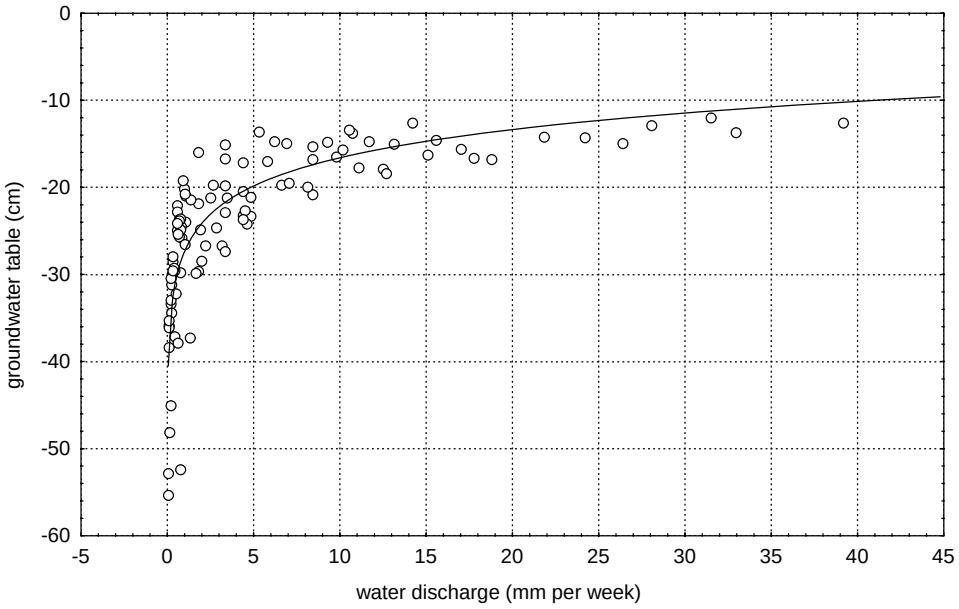

Fig. 1. Relationship between water discharge and actual level of groundwater table for bog pine forest.

Table 1. Selected levels of groundwater table and their week changes, week sums of total precipitation and water discharge for bog pine forest (BP) and for regenereted site (RS). GWT* illustrates the groundwater table level in the beginning of the appropriate week period, Δ GWT the week change of the groundwater table level, the positive value represents the elevation, the negative one the decline.

date	GWT* BP (cm)	GWT* RS	total precipitation (mm per week)	water discharge	Δ GWT BP (cm)	Δ GWT RS
15.5.95	-32.7	–	60.2	32.4	13.0	–
25.12.95	-23.5	0.0	19.0	68.5	5.8	0.5
6.5.96	-19.5	4.0	76.1	48.2	1.5	-1.0
20.5.96	-17.3	5.0	93.0	71.4	1.7	0.0
21.10.96	-21.5	0.5	55.5	79.1	8.1	0.5
7.7.97	-38.9	-7.5	73.4	9.7	22.2	8.5
21.7.97	-22.7	0.5	84.3	57.5	7.7	4.0

Reactions of the bog ecosystem to two downpour rainfalls are given in Fig. 2. This illustrates the groundwater level fluctuations in two sites (bog pine forest and a regenerated site with *Eriophoro vaginati-Sphagnetum* community, respectively), and week values of total precipitation and water discharge during the vegetation season in the 1997, when parts of central Europe were flooded. The groundwater level was highest in the beginning of the vegetation period (April 7). From the end of April, a stepwise decrease of stored water occured in both stands, due to the small amount of precipitation. By the end of June, the groundwater table level was 39 cm below the surface in the bog pine forest and 8 cm in the regenerated site. Total precipitation, of about 73 mm, was recorded during the next week (July 1–7). This rainfall event resulted in the peat profile becoming saturated, with the groundwater table reaching its maximum level since early April, and with very low outflows (9.7 mm per week). In the period of July 14–21, the peat profile stayed well saturated, with the groundwater level at 22.7 cm below the ground surface in the bog pine forest. Most of the downpour rainfall during this week (84 mm) discharged from the bog reservoir (57.5 mm per week) and only small changes to the water table were measured (+7.7 cm).

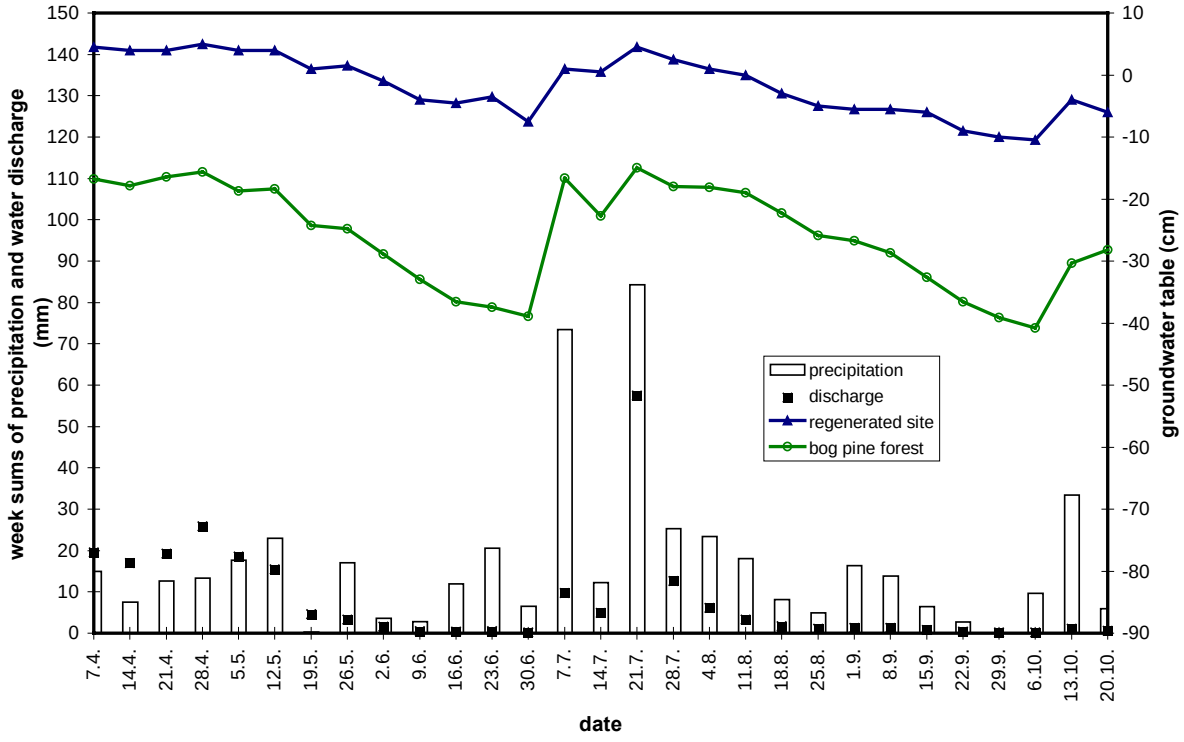

Fig. 2. Total week precipitation, water discharge and fluctuations of groundwater table for two sites (bog pine forest and regenerated site) during vegetation period in the 1997.

Discussion

In summer, water tables were found to be very sensitive to evapotranspiration (Heikurainen 1963), as evapotranspiration is a major item in the bog water balance, depleting the moisture content in the upper part of the peat profile. Since the discharge of water from the bog pine forest declines exceedingly when the groundwater table level is lower than 25 cm below the surface (see Fig. 1), the sharp decrease in the groundwater table, in the period from 2. 6. to 30. 6. 1997 and from 25. 8. to 6. 10. 1997 (Fig. 2), can be accounted for by evapotranspiration.

For these periods, the evapotranspiration was estimated as a residual term in the catchment water balance. Daily mean values of evapotranspiration for these periods are counted approximately 1.36 and 1.03 mm, respectively. The values of evapotranspiration in other studies are in same order of magnitude, but almost higher (*e. g.,* the mean value of May to October rate for E was 2,01 $mmday^{-1}$ in Eggelsmann 1964 or 2.7 $mmday^{-1}$ in Belotserkovskaja 1975); probably being in consequence with absence of the data for changes in soil water content in our estimation. The typical feature of summer hydrographs is the tendency for discharge to fall to low values after relatively brief period (cf. Fig. 2, Juni 2–16, September 22–October 6). Two weeks without rain (or only with low precipitation) may often suffice this effect; also other studies confirm the same feature (Eggelsmann 1964, Ferda and Pasák 1969).

However, the retention ability of the bog pine ecosystem is higher during the vegetation season, resulting from the periodic decline in the groundwater table due to intensive evapotranspiration. Some other processes connect bog water table with water balance in winter. During the winter months, when the peat profile is saturated by water and the groundwater table is near the surface, most of the rainfall water is discharged from the frozen bog surface; consequently the bog´s retention ability is very low.

The very thinness of the acrotelm to which the water-table movement is confined implies that most mires have a limited capacity either to store or to release water in the short term (Eggelsmann 1971). The low capacity of intact mires for temporary storage is confirmed also in other studies (*e. g.* Ferda and Pasák 1969, Ingram 1983, Quinton and Roulet 1998).

Conclusion

Generally, the retention ability of a continental raised bog, of which Červené blato bog is a good example, differs greatly during the year, being higher in the vegetation season, in consequence of the periodic decline of the groundwater table due to intensive evapotranspiration. During the winter months, when the peat profile is saturated by water and the groundwater table is near the surface, most of the rainfall water is discharged from the frozen bog surface; consequently the bog´s retention ability is very lower.

These results hold especially for actively growing ombrogenous bogs with a generous acrotelm. In the case when the bog ecosystem is strongly influenced by drainage or opencut peat mining, and the acrotelm is reduced or removed, the bog surface is formed by a frequently dry, impermeable layer of peat with very low possibility to absorb the precipitation. Therefore, all surplus water is quickly discharged from the bog reservoir. In opposite, moderately drained bogs are better water reservoir than intact one due to higher thickness of their acrotelm (cf. Ferda and Pasák 1969 etc.).

The idea that intact mires act as useful water storage reservoir reducing runoff is sometimes still used as an argument for their conservation, but this argument seems to be incorrect. From the hydrological point of view, the case for mire conservation are more in water quality then in high retention ability. The role of mires in short water cycle, i. e. their evapotranspiration should be studied and quantitavely evaluted for the temperate zone.

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Employment

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